U.S. Department
of Commerce

Volume 88
Number 2, 1990

Fishery Bulletin

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, BIN C15700, Seattle, WA 98115-0070. Second class postage is paid in Seattle, Wash., and additional offices. POSTMASTER: send address changes for subscriptions to Fishery Bulletin, Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402.

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The Secretary of Commerce has determined that the publication of this periodical is necessary in the transaction of the public business required by law of this Department. Use of funds for printing of this periodical has been approved by the Director of the Office of Management and Budget.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. Subscription price per year: $18.00 domestic and $20.00 foreign. Cost per single issue: $5.00 domestic and $11.25 foreign.

The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

U.S. Department of Commerce
Seattle, Washington

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A Comparative Study of Habitat Use by Young-of-the-year, Subadult, and Adult Rockfishes on Four Habitat Types in Central Puget Sound*

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Abstract.– Seasonal habitat use of young-of-the-year, subadult, and adult rockfishes (*Sebastes caurinus*, *S. maliger*, and *S. auriculatus*) were compared for four habitat types: high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass. Diving surveys conducted December 1986 through October 1988 on two representative sites of each habitat type revealed significant seasonal changes in rockfish densities and habitat use. Young-of-the-year (YOY) recruitment varied between the two survey years: YOY were observed on all habitat types in the summer and fall of 1987, whereas they were observed at only one site (artificial reef) in a similar time period of 1988. High-relief rocky reefs had the most consistent densities of the three rockfish species, mostly fish >200 mm TL. Adult and YOY copper, quillback, and brown rockfishes were observed on the low-relief rocky reefs primarily in the summer months coincident with summer algal growth; when the kelp died back in the fall, most rockfishes left these reefs. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect) and large copper rockfish (up to 56.3/transect), were observed on the artificial reefs. Here, also, density fluctuations were dramatic; copper rockfish densities peaked in fall and winter and declined (to 0/transect) during the summer, and quillback rockfish densities also seasonally fluctuated. Sand/eelgrass areas were the least-utilized habitat type; only during July and August were young-of-the-year and low densities of adult copper and brown rockfishes observed on one sand/eelgrass site. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus, the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

Manuscript accepted 1 December 1989.
Fishery Bulletin, U.S. 88:223–239.

Rockfishes are a successful group of marine fishes represented by about 100 species (Barsukov 1981), which occupy a variety of habitats ranging from the intertidal to the edge of the continental shelf (Lea 1983). This speciose and interesting group displays extremes in habitat use and movement patterns: Some species live deep (500 m) over sandy bottoms, some make long-distance movements (to 550 km), whereas others are perennially sedentary on shallow (<10 m) rocky reefs (Larson 1980, Love 1980, Culver 1987). One group of rockfishes is solitary and demersal and inhabits shallow reefs (Ebeling et al. 1980a); in Puget Sound this group of rockfishes is represented by copper *Sebastes caurinus*, quillback *S. maliger*, and brown *S. auriculatus*.

Copper, quillback, and brown rockfishes are common shallow-water benthic species found along the Pacific coast of North America (Hart 1973). They are morphologically similar to one another but differ in coloration. The three species have overlapping geographic ranges; copper and brown rockfishes are found from Baja California to Alaska, whereas quillback are found from central California to Alaska (Hart 1973). All three species occur in Puget Sound, Washington, and comprise approximately 25% of the recreational bottomfish catch in central Puget Sound (Palsson 1988). These species inhabit a variety of habitat types although highest densities are reported on artificial reefs, natural rocky reefs, and rock piles in water less than 30 m (Moulton 1977, Buckley and Hueckel 1985). Usually these species are found directly on the bottom closely associated with rock, artificial substrate, or vegetation (Patten 1973, Moulton 1977). Although copper and quillback rockfishes are common throughout Puget Sound, the San Juan Islands, and Strait of Juan de Fuca, brown rockfish are more limited in distribution and are found only within central and south Puget Sound (Moulton 1977).

Rockfishes are viviparous (Boehlert and Yoklavich 1984), undergoing internal fertilization and subsequently releasing pelagic larvae. Little is known regarding the length of time that young rockfishes are pelagic before they recruit to adult or transitional habitat. Parturition reportedly occurs April through June for the three species in Puget Sound (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). An influx of postlarval or young-of-the-year (YOY) rockfishes into isolated areas in Puget Sound has been observed (Patten 1973, Gowan 1983); assessment of habitat

*Contribution No. 804 of the School of Fisheries, University of Washington.

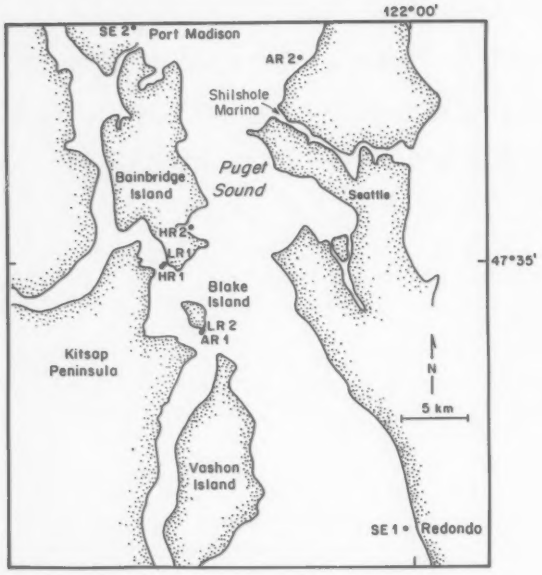

Figure 1

Map of study sites within central Puget Sound. HR1 Orchard Rocks, HR2 Blakely Point, LR1 Bainbridge Island, LR2 Blake Island, AR1 Blake Island, AR2 Boeing Creek, SE1 Redondo, SE2 Port Madison.

features required by recruits and different habitats utilized has been only qualitatively described. It is likely that habitat requirements of juveniles and adults differ, as juveniles may require shelter from predation and associate more closely with structural algal cover (Hobson 1972, Carr 1989). Ebeling and Laur (1985) experimentally demonstrated that young surfperches sought and were restricted to microhabitats that offered protection from predation. Carr (1983) suggested that kelp may provide a refuge from predation for YOY rockfishes including three species found offshore as adults (*Sebastes paucispinus*, *S. pinniger*, and *S. miniatus*), that recruit to kelp beds in central California. Because rockfish produce pelagically dispersed larvae and juveniles, local adult density is probably a poor predictor of local recruitment and future adult density. Rather, the limited availability of habitat with which young-of-the-year and juvenile associate may be the critical determinant of local recruitment. Determining the habitat requirements of young rockfishes can be crucial to our understanding of local rockfish dynamics. If algae, seagrasses, or other habitats provide YOY rockfishes essential shelter from predation and increased access to food, then recruitment could be suppressed by eliminating such shelter or enhanced by adding more shelter. Habitat affinities and requirements are an unknown for YOY and juvenile rockfishes in Puget Sound.

Copper, quillback, and brown rockfishes inhabit a variety of habitats, yet the relative importance of each habitat and seasonal uses are unknown. Additionally, differences in habitat use by different life-history stages are poorly understood. For example, do young rockfishes settle on reefs and remain there for life, or do the different age groups (young-of-the-year, subadult, and adult) later move to separate or different habitats? Understanding how and when the different habitats are exploited provides needed information on ecological requirements for habitat management; recognition and protection of important habitats are necessary for effective fisheries management. Similarly, further descriptions of the different habitats are required to adequately assess the relative importance of habitat features to the different life-history stages of rockfishes. This study was designed to provide a quantitative comparison of habitat use for copper, quillback, and brown rockfishes on four habitat types common in Puget Sound.

Materials and methods

Study sites

For each of four habitat types—high-relief rocky reef, low-relief rocky reef, high-relief artificial reef, and sand/eelgrass—two representative replicate study sites were selected. The two high-relief natural rocky reefs were characterized by steep vertical relief to 5 m off the bottom, surface canopies of the annual bull kelp *Nereocystis leutkeana* May through November, and understories of the perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. The high-relief rocky reefs range in depth from 12–20 m (gauged from mean lower low water). The Orchard Rocks high-relief rocky reef (HR1) is located on the southeastern side of Bainbridge Island (Fig. 1) approximately 600 m offshore in the middle of Rich Passage, which is swept by high currents up to 8.1 km/hour (4.5 knots) (U.S. Dep. Commer. 1987, current tables). The entire Orchard Rocks reef covers approximately 5 ha. The portion of reef used as the study site was about 12–18 m in depth and consisted of large boulders and rocky ledges that rise up to 5 m off the bottom. The second high-relief reef (HR2), Blakely Point, is a series of rock outcroppings separated by sand and shell gravel. The outcroppings are oriented perpendicularly offshore from the north entrance of Port Blakely Harbor on the eastern side of Bainbridge Island. Transects extended across the reef from 12–18 m in depth; each transect covered a similar depth range. Similar to HR1, the HR2 reef consists of steep walls and crevices with vertical relief of 5 m, but has minimal current.

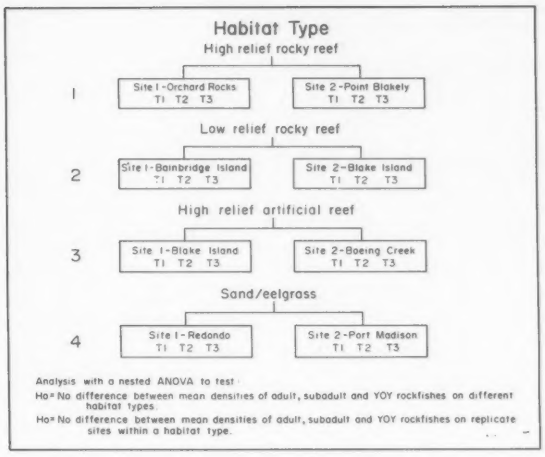
Habitat Type
High relief rocky reef
1
Site 1 - Orchard Rocks
T1 T2 T3
Site 2 - Point Blakely
T1 T2 T3
Low relief rocky reef
2
Site 1 - Bainbridge Island
T1 T2 T3
Site 2 - Blake Island
T1 T2 T3
High relief artificial reef
3
Site 1 - Blake Island
T1 T2 T3
Site 2 - Boeing Creek
T1 T2 T3
Sand/eelgrass
4
Site 1 - Redondo
T1 T2 T3
Site 2 - Port Madison
T1 T2 T3
Analysis with a nested ANOVA to test:
Ho= No difference between mean densities of adult, subadult and YOY rockfishes on different habitat types.
Ho= No difference between mean densities of adult, subadult and YOY rockfishes on replicate sites within a habitat type.

Figure 2
Nested experimental design showing habitat types in central Puget Sound, sites within habitat types, and the three transects per site.

The two low-relief rocky reefs were characterized by flat, featureless cobble and rock bottom with a few isolated areas of vertical relief (1–2 m). Transects extended from 8–10 m in depth, but not deeper than 10 m where the reef drops off into sand/cobble substrate. The low-relief reefs were more uniform in depth when compared with the high-relief reefs. Both low-relief reefs have dense canopies of *Nereocystis leutkeana* May through November and understories of perennial kelps *Agarum fimbriatum* and *Pterygophora californica*. Low-relief habitats underwent dramatic changes in the fall and winter when they were virtually devoid of all fish and algal structure. Bainbridge Island low-relief rocky reef (LR1) is 500 m inshore from HR1, and the two reefs are separated by cobble and sand. Blake Island low-relief reef (LR2) is located 5 km south of Bainbridge Island. Both low-relief reefs are swept by high currents up to 8.1 km/hour (4.5 knots).

The two high-relief artificial reefs were characterized by vertical relief of up to 5 m and no surface canopies of bull kelp, but with isolated patches of understory kelps. Transects extended from 15–20 m in depth. The Blake Island artificial reef (AR1) was constructed in 1980 (Laufle 1982) and is located 5 km south of Bainbridge Island on the southwestern side of Blake Island approximately 500 m offshore of LR1. The reef consists of concrete rubble, slabs, rectangular boxes, and tires forming vertical relief up to 4 m. The Boeing Creek artificial reef (AR2) was constructed in late 1982 and is located 8 km north of Shilshole marina approximately 600 m offshore. The reef consists of concrete rubble with vertical relief of up to 6 m. The two reefs differ, as Blake Island is swept by strong currents up to 8.1 km/hour (4.5 knots) while Boeing Creek experiences little current.

The sand/eelgrass areas were characterized by flat, shallow, unconsolidated substrate with dense growth of eelgrass *Zostera marina* May through November. Eelgrass typically grows in low-current, sheltered water and is restricted to depths less than 6 m (Phillips 1984), so the transects were placed at 5 m. The Redondo (SE1) sand/eelgrass area is located approximately 500 m north of Saltwater State Park, 24 km south of Seattle. The Port Madison eelgrass area (SE2) is located 500 m north of the Suquamish boat ramp, off the northern side of Bainbridge Island.

Survey methods

From December 1986 through February 1988, I conducted monthly SCUBA surveys and estimated rockfish densities along three (30-m long, 3 m wide, and 1 m high) permanent transect lines at each of the eight reefs (Fig. 2). After the February 1988 survey, surveys were conducted in April, June, July, and August of 1988. In October 1988, surveys quantifying only YOY rockfishes were conducted on four reefs where YOY had been observed in the summer and fall of 1987: HR2, LR1, AR2, and SE2. All eight sites were sampled each month, and all three transects were sampled on the same day. I swam along the transect line and recorded individuals of each species as YOY (<80 mm TL), subadult (80–200 mm TL), and adult (>200 mm TL). During the summer and early fall when kelp cover was the highest, I also swam through the canopy to search for YOY rockfish. The ability to designate these size categories was verified by periodically capturing and measuring fish. Because YOY copper, quillback, and brown rockfishes could not be identified to species underwater, they were combined into one group. A total of 456 transects was completed on all reefs: 24 transects conducted monthly for 15 consecutive months December 1986–February 1988, and 24 transects conducted monthly during April, June, July, and August 1988. Fifteen additional YOY surveys were completed in October 1988.

Other information collected along the transect lines included estimates of vegetative cover and water temperature. Kelp and eelgrass cover was qualitatively assessed by estimating, at the end of each transect, the percent cover of bullkelp, understory kelps, and the height of eelgrass present. The percent cover ranged from 0 (no vegetation present) to 100% (transect line completely covered by vegetation). Temperatures were recorded along the transect lines on each survey with a submersible thermometer.

Survey analyses

From the three transects at each site, a mean number (±95% CI) of fish per transect was computed for each species and size category. To determine whether densities of rockfishes differed among the four habitat types and within the two replicate sites within each habitat type, I used a nested analysis of variance (ANOVA) (Zar 1984) (Fig. 2) that tested two null hypotheses: (1) There is no difference in rockfish densities between habitats ($F_{0.05(1)3\text{(habitat types)},4\text{(sites)}}$), and (2) there is no difference in rockfish densities between the two replicate sites within each habitat type ($F_{0.05(1)4\text{(sites)},16\text{(error)}}$). The degrees of freedom for error was calculated as (4(types) · 2(sites) · 3(transects) – 4 · 2) = 16 (Zar 1984, p. 147). To reduce the number of analyses, data were analyzed as a separate ANOVA for each of six seasonal periods using the middle month: Winter 1 = December 1986–February 1987; spring = March 1987–May 1987; summer 1 = June 1987–August 1987; fall = September 1987–November 1987; winter 2 = December 1987–February 1988; and summer 2 = June 1988–August 1988. Although density estimates were similar within quarters (Figs. 3–6), the sedentary behavior of rockfish could mean that the same individuals were counted in February that had previously been counted in January, which would constitute a repeated sample. Thus to eliminate the possibility of non-independence of data, as I have no evidence that rockfish redistribute themselves randomly from month to month, I used only the middle month of each quarter. Because many months and sites contained zero densities and, in some cases, the variances were proportional to the means, the data were transformed using a square root transformation (X' = square root (X + 0.5)). If a significant difference in densities was detected among the four habitat types, the types were then compared using Tukey's multiple range test (Zar 1984) to determine which types were different.

To determine whether densities were different between years at each site, quarterly estimates were compared using a Student's t-test (Zar 1984). For these tests, densities from the summer of 1987 were compared with the summer of 1988 for each site testing the null hypothesis: There is no difference between densities of each site between summer 1987 and summer 1988. Similarly, densities from the winter of 1987 were compared with the winter of 1988. I conducted individual tests for copper, quillback, brown, and YOY rockfishes for summer and winter comparisons.

Results

Habitat type and site comparisons

All size categories of copper, quillback, and brown rockfishes and YOY rockfish were seen at the high-relief natural habitat type (Fig. 3). Consistent monthly densities of large (>200 mm) copper (mean 3.7–13.0 fish/90-m^3 transect) and quillback (mean 3.0–7.0 fish/transect) rockfishes were observed throughout the year on the high-relief rocky reefs. Brown rockfish (>200 mm) (mean 1.3–4.0 fish/transect) were seen at HR1 (Orchard Rocks) but infrequently at HR2 (Blakely Point). Low densities (mean<1.3 fish/transect) of subadult (80–200 mm) copper, quillback, and brown rockfishes were observed on both reefs until the late summer and fall 1987. YOY (<80 mm) rockfishes were observed (mean 8.0–57.0 fish/transect) from August–November 1987 but only on HR2. YOY were not observed in the summer or fall of 1988. After the influx of YOY during summer and fall 1987 on HR2, an increase in 80–200 mm rockfishes was subsequently observed (mean 6.0–15.0 fish/transect).

Rockfishes primarily utilized low-relief rocky reefs during the summer, coincident with peak *Nereocystis leutkeana* and understory cover, and were infrequently observed during other seasons (Fig. 4). Large copper (up to a mean 6.0 fish/transect) and brown rockfishes (up to a mean 7.7 fish/transect) were observed mainly during the summer, whereas large quillback rockfish were not seen at LR1 and only infrequently at LR2. Low densities (mean 0–3.3 fish/transect) of small copper and quillback rockfishes were seen on LR2, while small brown rockfish were never seen on either reef. YOY rockfishes were observed (mean 16.7 fish/transect) during August 1987 on LR1 and (mean 1.3 fish/transect) on LR2 during October 1987, but not during the summer or October of 1988.

On the artificial reefs, densities of large copper rockfish fluctuated throughout the year. During both 1987 and 1988, high densities (mean 12.0–56.3 fish/transect) were seen September through May; however, low densities (mean 0.3–2.3 fish/transect) of copper rockfish were observed June through August (Fig. 5). Variable densities (mean 0–12.3 fish/transect) of large quillback rockfish were observed on AR1 while they were lower in number (mean 0–2.3 fish/transect) on AR2 (Fig. 5). Large brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. Low densities (mean 0–5.0 fish/transect) of subadult (80–200 mm) copper rockfishes were observed on both artificial reefs throughout the year. Extremely high densities (mean 8.0–420.0 fish/transect) of subadult quillback rockfish were observed on both AR1 and AR2, although densities were much higher on AR2 (up to 420

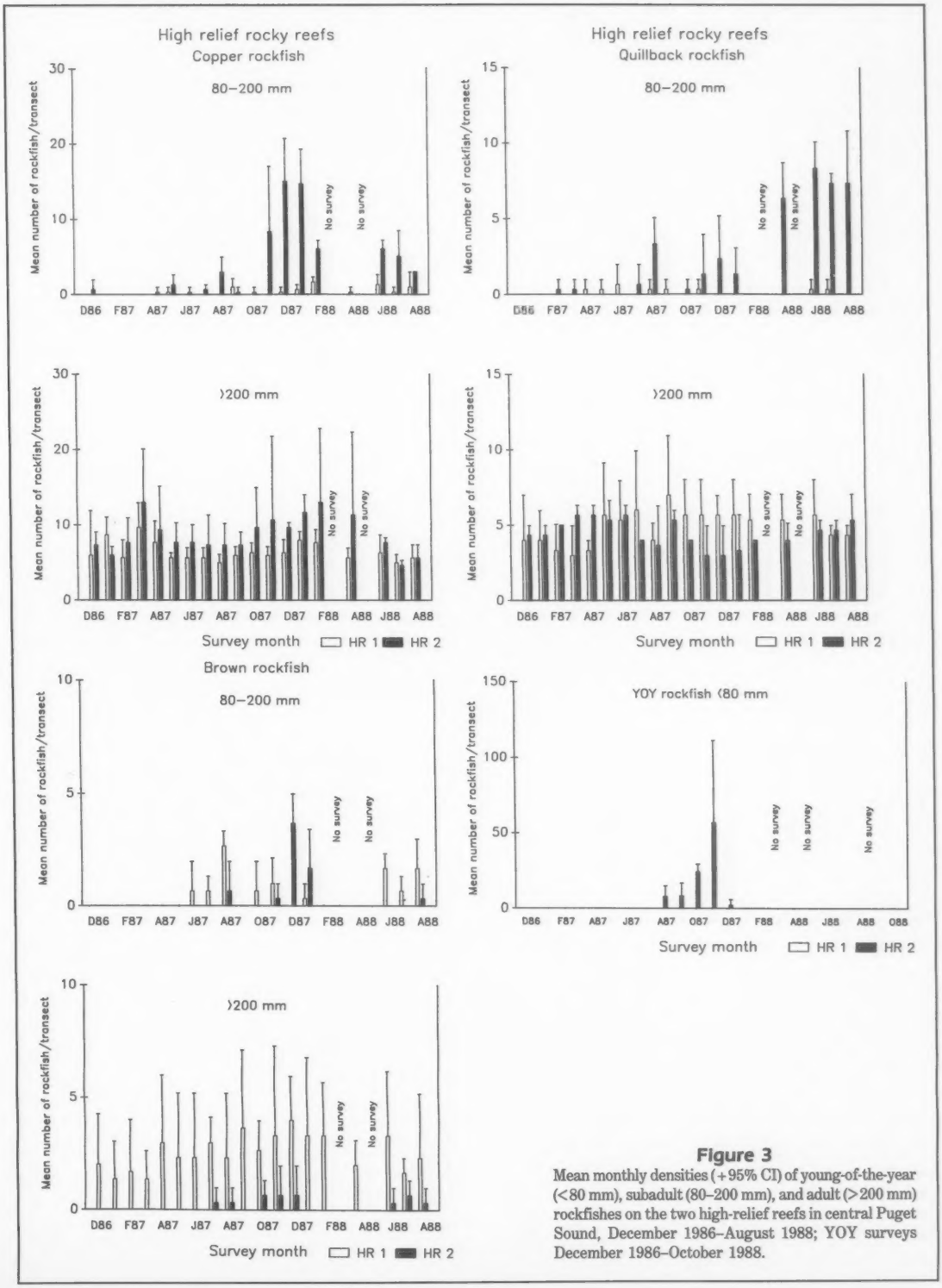

Figure 3

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two high-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

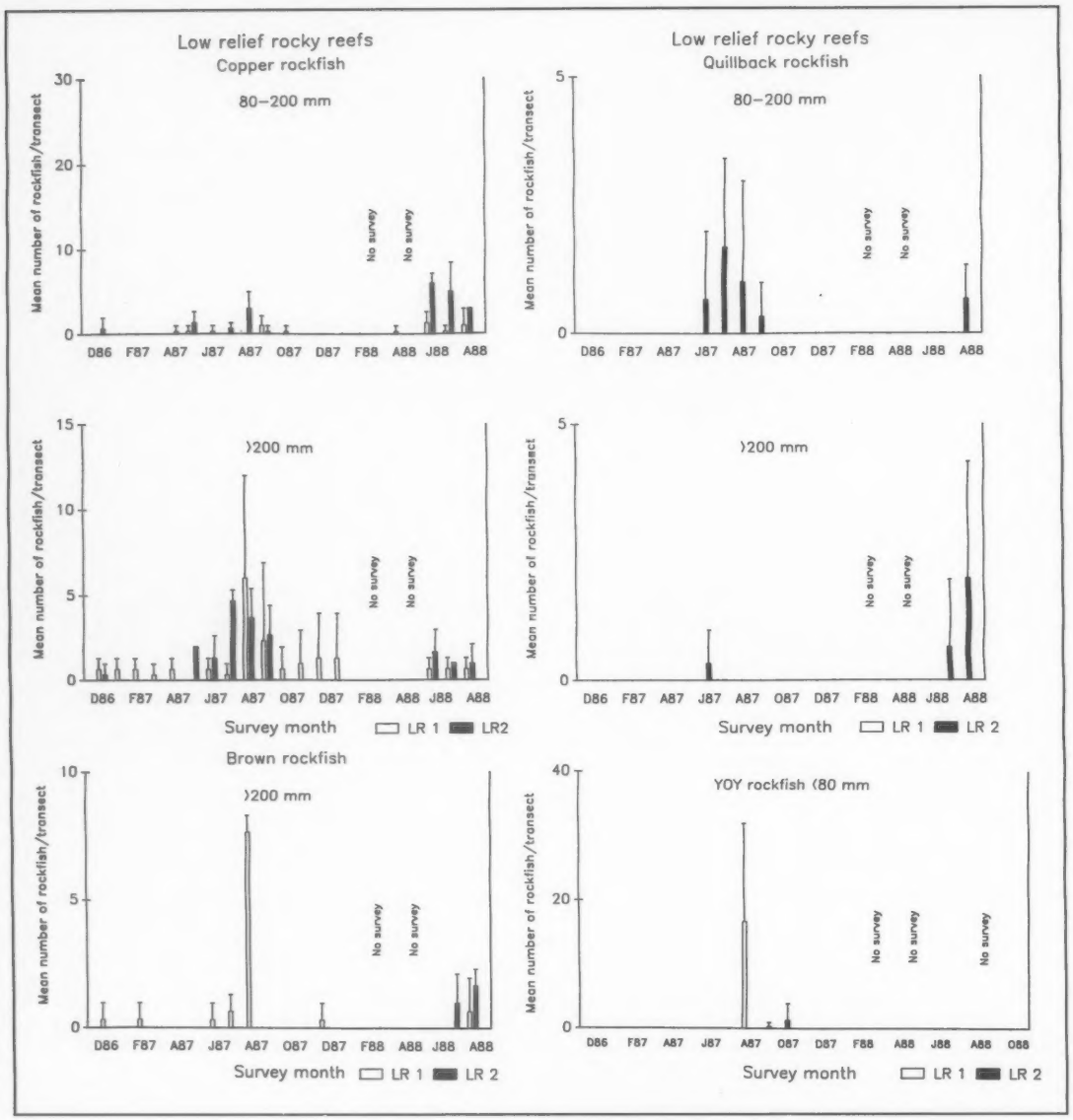

Figure 4

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two low-relief reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No subadult brown rockfish were observed.

fish/transect). Small brown rockfish were infrequently (mean 0–0.3 fish/transect) seen on either artificial reef. YOY rockfishes were observed (mean 1.7–63.0 fish/transect) only on AR2 during the spring of 1987, and during the following fall, winter, spring, and summer (mean 4.3–80.0 fish/transect). Low densities (mean 2.0 fish/transect) were observed in the October 1988 survey. YOY were never observed on AR1.

Sand/eelgrass areas had the lowest densities of all habitats sampled; large copper rockfish (mean 5.0 in July 1987, mean 0.7 in August 1988), brown rockfish (mean 1.0, August 1987) and YOY (mean 111.0, July

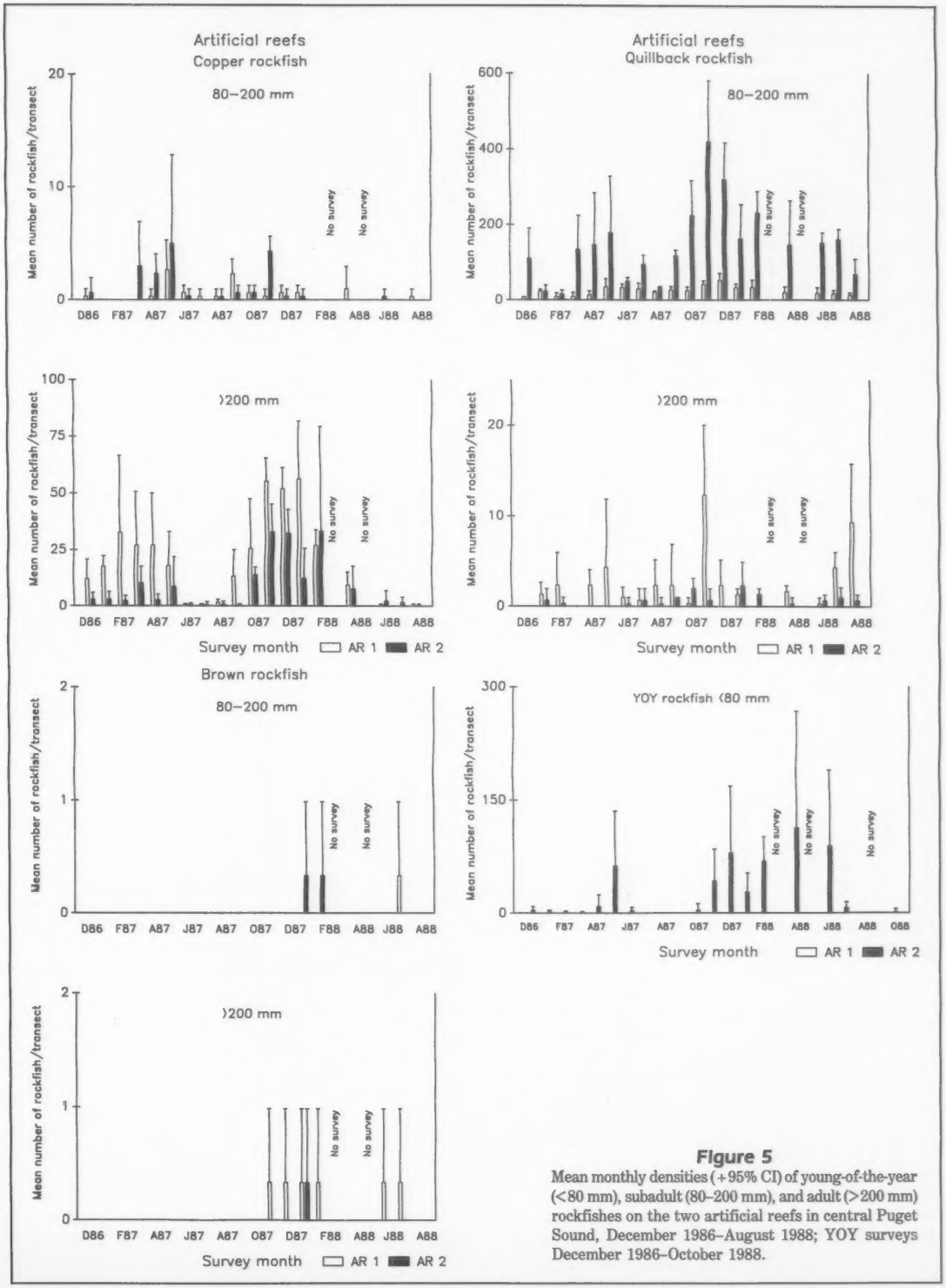

Figure 5

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two artificial reefs in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988.

1987) were the only rockfishes seen and only during surveys conducted in late July and August (Fig. 6). These observations of rockfishes coincided with the peak growth of eelgrass up to 1.5 m high; in the fall and winter the height of eelgrass beds was reduced to <0.5 m. No quillback rockfish were ever observed on sand/eelgrass.

Nested analysis of variance

Habitat type comparison When density differences were detected, the highest densities were observed on the high-relief rocky and artificial reefs ($P<0.05$ nested ANOVA, Table 1). Highest densities of large copper rockfish were observed on high-relief rocky reefs during both the summer of 1987 and 1988, whereas artificial reefs had the highest densities in the fall and winter. Similar low densities of 80–200 mm copper rockfish were observed on all four habitat types all seasons except fall 1987. High-relief rocky reefs had the highest densities of large quillback rockfish all seasons; sand/eelgrass and low-relief rocky reefs were similar as large quillback rockfish were rarely observed. Artificial reefs had the highest densities of 80–200 mm quillback rockfish all seasons except winter and summer 1988. No density differences were observed for both size groups of brown rockfish on any of the habitat types. Similarly, YOY rockfishes were observed on all four habitat types, and no differences were detected in densities of YOY rockfish among the four habitats.

Replicate site comparison For many (23/42 groups) size groups of copper, quillback, brown, and YOY rockfishes, there were significant differences in densities between the two replicate sites for most seasons ($P<0.05$ nested ANOVA, Table 1). The major exception was that similar densities of large copper rockfish were observed on replicate sites all seasons except spring 1987.

Year-to-year comparison

For most size categories of copper, quillback, and brown rockfishes, there were no significant difference between their densities for the two periods tested: Summer 1987–summer 1988, and winter 1987–winter 1988 (Table 2). For the summer comparisons, the principal differences in densities were for YOY rockfish on all sites where they were observed: HR2, LR1, LR2, AR2, and SE2. YOY were observed at all five reefs in the summer of 1987; however, no YOY were observed in the summer of 1988, except at AR2. Other differences between summer 1987–1988 densities were 80–200 mm quillback rockfish on HR2; densities of small quillback rockfish were higher in the summer of 1988 after the YOY recruitment of 1987.

Similar to the summer 1987–summer 1988 comparisons, there were few significant density differences for winter 1987–winter 1988 (Table 2). The principal differences were that large copper rockfish and small

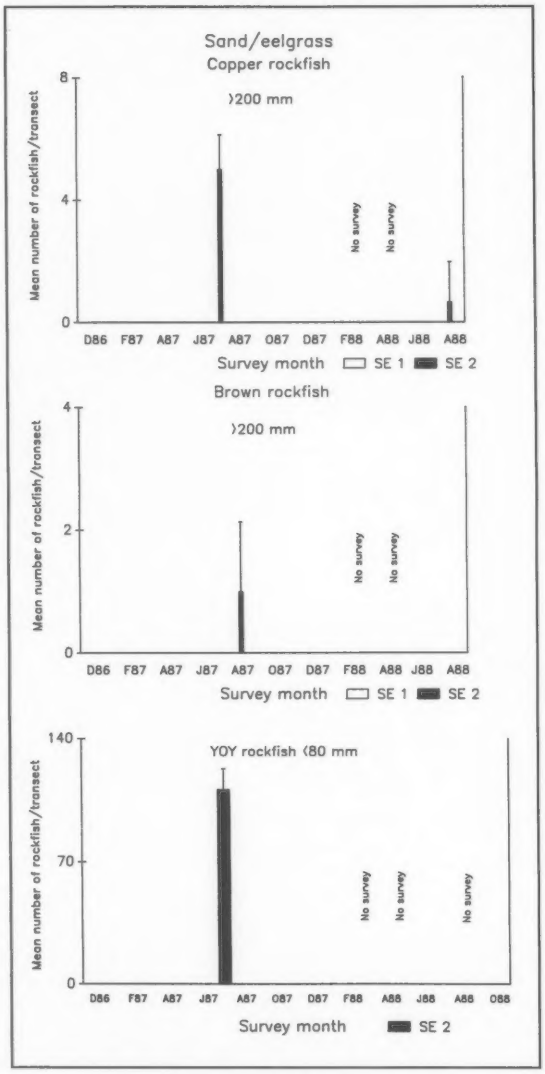

Figure 6

Mean monthly densities (+95% CI) of young-of-the-year (<80 mm), subadult (80–200 mm), and adult (>200 mm) rockfishes on the two sand/eelgrass areas in central Puget Sound, December 1986–August 1988; YOY surveys December 1986–October 1988. No quillback rockfish (80–200 mm or >200 mm), subadult copper rockfish, or subadult brown rockfish were observed.

Table 1

Results of the nested ANOVAs ($P<0.05$) testing for differences between rockfish densities among the four habitat types: High-relief rocky reef (HR), low-relief rocky reef (LR), high-relief artificial reef (AR), and sand/eelgrass (SE). If there was a significant difference between type densities (Test 1), the results of Tukey's multiple range test are listed from highest to lowest densities. Test 2 lists the significant differences (*) in densities between sites.

	Copper		Quillback		Brown		Young-of-the-year
	80–200	>200 mm	80–200 mm	>200 mm	80–200 mm	>200 mm	<80 mm
Test 1							
1987							
Winter			AR>HR>SE=LR	HR>AR>LR=SE			
Spring			AR>HR>SE=LR	HR>AR>LR=SE			
Summer		HR>LR>AR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
Fall	AR>HR>LR=SE	AR>HR>LR=SE	AR>HR>SE=LR	HR>AR>LR=SE			
1988							
Winter		AR>HR>LR=SE		HR>AR>LR=SE			
Summer		HR>LR>AR=SE		HR>AR>LR=SE			
Test 2							
1987							
Winter							*
Spring	*	*	*	*		*	
Summer			*		*	*	*
Fall			*	*		*	*
1988							
Winter	*		*			*	*
Summer	*		*	*		*	*

Table 2

Summary of year-to-year comparisons testing (Student's t-test) for differences in rockfish densities between summer (June, July, Aug.) 1987–summer 1988 and winter (Dec., Jan., Feb.) 1987–winter 1988. Listed are habitat types where a significant difference was detected. HR = high-relief rocky reef, AR = high-relief artificial reef, LR = low-relief rocky reef, SE = sand/eelgrass.

	Summer 1987–Summer 1988	Winter 1987–Winter 1988
Copper		
80–200 mm	HR2	HR2
>200 mm	AR1	HR2, AR1, AR2
Quillback		
80–200 mm	HR2, AR1, AR2	AR1, AR2
>200 mm	No differences	HR1
Brown		
80-200 mm	No differences	HR2
>200 mm	LR1	No differences
Young-of-the-year		
<80 mm	HR2, LR1, LR2, AR2, SE2	AR2

quillback rockfish densities were higher in the winter of 1988 on both artificial reefs. In addition, both small and large copper rockfish increased on HR2.

Species comparison

Small copper rockfish were infrequently seen on any habitat (Figs. 3–6). Small copper rockfish were first observed on the high-relief rocky reefs after the influx of YOY in the fall and winter. They were also sporadically observed on the artificial reefs and Blake Island low-relief reef. Large copper rockfish were seen on all habitat types and were observed all seasons. Consistent densities of large copper rockfish were observed

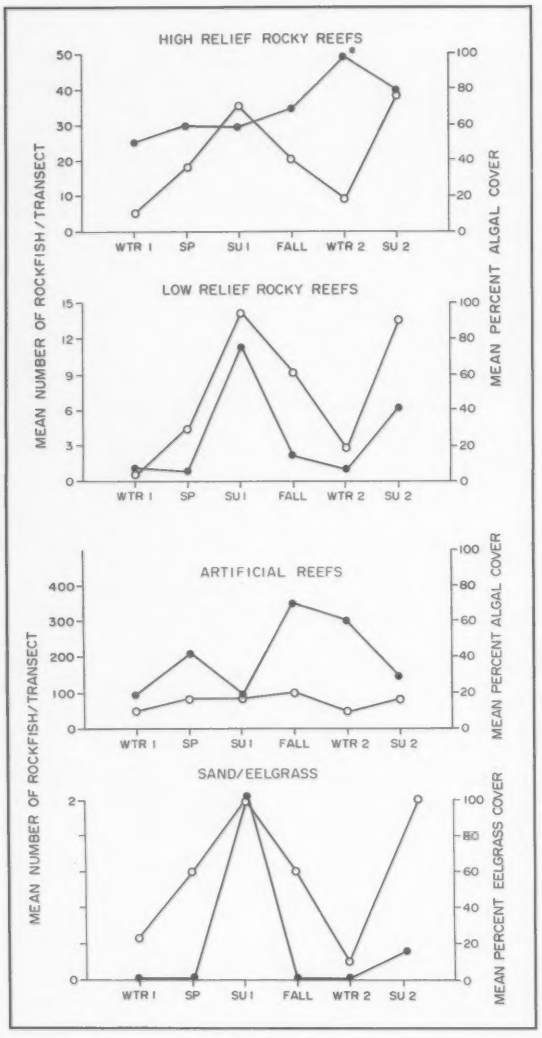

Figure 7

Mean percent of algal or eelgrass cover (O) compared with mean number (●, combination of 80–200 mm and >200 mm) of copper, quillback, and brown rockfishes on the four habitat types in central Puget Sound for winter 1 (wtr1), spring (sp), summer 1 (su1), fall (fall), winter 2 (wtr2), and summer 2 (su2). Seasons are described in Methods section. Density increase in high-relief rockfish (*) followed the influx of young-of-the-year rockfish. Percent eelgrass cover was relative to maximum height (1.5 m) of eelgrass which occurred during the summer.

on the high-relief reefs all seasons. In contrast, their densities fluctuated seasonally on other habitats; they were only observed during the summer and fall on the low-relief reefs during all seasons, although in lower densities during the summer on the artificial reefs, and only during the summer on the sand/eelgrass.

Small quillback rockfish were primarily observed on the artificial reefs all seasons and were infrequently observed on all other habitats (Figs. 3–5). Large quillback rockfish were most common on the high-relief rocky reefs and artificial reefs. Large quillback rockfish were rarely observed on the low-relief reefs. Neither small nor large quillback rockfish were observed on the sand/eelgrass.

Small brown rockfish were observed only on the high-relief reefs and on one artificial reef (Figs. 3, 5). Large brown rockfish were seen all seasons on the high-relief reefs although highest numbers were observed at HR1 (Orchard Rocks) (Fig. 3). They were also seen during the summer on low-relief reefs and sand/eelgrass (Figs. 4, 6).

YOY rockfish were observed on all four habitat types (Figs. 3–6). On the high-relief, low-relief reefs, and the sand/eelgrass, they were first seen in the summer and fall of 1987. YOY were observed year-round on Boeing Creek artificial reef. YOY were not observed in the summer or October of 1988 except at AR2.

Macrophyte cover varied seasonally; the densest cover was observed June through October on all reefs (Fig. 7). The high-relief reefs had dense canopies of *Nereocystis leutkeana* and subcanopies of *Pterygophora californica*, and *Agarum* that during the summer covered 50–100% of the bottom along the transect lines. The two low-relief reefs had 100% bullkelp and understory coverage June through October. The annual bullkelp was gone November through May and only the stipes of the understory perennial kelps remained; the blades of the understory kelps had eroded or were otherwise lost. There was no *Nereocystis* on the two artificial reefs; however, understory kelps covered approximately 0–20% of the transects, with peak growth in the summer. Sand/eelgrass transects were always covered with the perennial eelgrass throughout the year, although the height varied seasonally. The height peaked during the summer at approximately 1.5 m, and during the winter many of the blades were gone and the eelgrass was prostrate with little (0–0.5 m) vertical structure.

Monthly mean temperatures were highest August through October (up to 13°C) and lowest (down to 7.1°C) in January and February (Fig. 8). There was little qualitative difference in temperatures between the different reefs, although depth ranges were 5–20 m along transect lines.

Discussion

Seasonal habitat use

Habitats that underwent seasonal vegetation and subsequent structural changes had the most dramatic

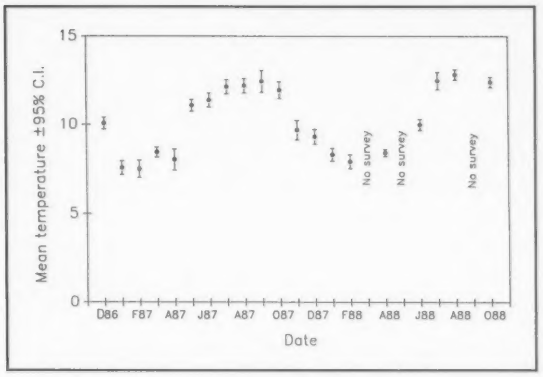

Figure 8
Mean monthly bottom temperatures (°C) ±95% CI measured along transect lines on the eight reefs in central Puget Sound, December 1986–October 1988.

density differences (Fig. 7). On the low-relief rocky reefs and sand/eelgrass, the highest densities, mainly >200 mm copper, brown, and YOY rockfishes, were observed during the summer coincident with the densest growth of bull kelp, understory kelps, and eelgrass. When the vegetation died back, lowest densities of rockfishes were observed, presumably due to movement away from the reefs. Movement away from the Blake Island low-relief reef in the fall onto the Blake Island artificial reef was confirmed in a tag-recapture study (Matthews In press). Richards (1987) also noted a decrease in copper rockfish densities off Vancouver Island during the winter, but argued that it was not fish movement that caused the decrease in densities but rather that during the winter fish were simply more difficult to see as they presumably hid in crevices. On the low-relief reefs and sand/eelgrass areas I surveyed, this explanation was not the case. Once the vegetation died back there were few places for fish to hide undetected by divers; there are no crevices or holes in the flat-bottom rock reef and sand. Fishing pressure was not responsible for the seasonal density fluctuations. Although I never directly measured the amount of fishing activity, I observed the highest number of sportfishing boats (both divers and anglers) at the high-relief reefs, whereas the lowest fishing effort occurred at the low-relief and artificial reefs. Larson and DeMartini (1984) compared two low-relief areas in southern California with and without giant kelp *Macrocystis pyrifera*. They found a higher biomass of fishes on the reef with kelp and concluded that the presence of kelp on low-relief reefs enhances fish biomass by providing prey and structure. The seasonal change in kelp on high-relief reefs had no effect on fish densities; presumably there is adequate structure (rocks and crevices) and prey on these reefs regardless of kelp cover. Other research in California has demonstrated that kelp on high-relief reefs had less effect on fish abundance when compared with their dramatic effect on low-relief reefs; when kelp cover declines on low-relief reefs, the shelter is lost but refuge in high-relief rock is permanent regardless of kelp cover (Quast 1968, Stephens et al. 1984, Ebeling and Laur 1988). Large (>200 mm) copper rockfish densities on the artificial reefs declined dramatically during the summer coincident with higher densities of large copper rockfish on the low-relief rocky reefs. Copper rockfish may leave the artificial reefs in the summer because of the lack of vegetation (bullkelp and understory kelps) and its associated prey. The summer is an important feeding time for rockfishes when fat reserves are stored to be used as energy sources during the winter (Guillemot et al. 1985). Although the artificial reefs had isolated patches of perennial kelps (*Agarum* and *Pterygophora*) during the summer, this habitat type had the sparsest vegetation growth of all the habitats surveyed. Because low-relief rocky reefs, artificial reefs, and sand/eelgrass were not suitable year-round habitats, rockfish move to utilize alternate habitats during the winter (Matthews In press).

Habitat comparison

Apparently, high-relief rocky reefs were suitable habitat for copper, quillback, brown, and YOY rockfishes: This was the only habitat type where all size categories of the three species as well as YOY were observed, although few were observed in the 80–200 mm range. Actually, one should not expect to see high numbers of 80–200 mm rockfish. Copper and quillback rockfishes are relatively slow-growing and may live up to 55 years (Richards and Cass 1987). Rockfishes release thousands of larvae, and the highest predation and mortality is on the youngest fish; presumably only a few survive to adults. Rockfish >200 mm represent several age groups—those rockfish about 5 years and older—whereas the 80–200 mm group represents only a few age classes of 1–5 years (Sandra Oxford, Wash. Dep. Fish., Seattle, WA 98115, pers. commun., summer 1988). Thus, one would expect to see more fish >200 mm than 80–200 mm on the high-relief natural reefs where the size groups co-occur. High-relief rocky reefs also had the most consistent densities of large rockfish and were the most structurally complex of all habitats surveyed. Although the vertical relief was similar to that on artificial reefs, natural rocky reefs had more cracks, crevices, and holes for fish to hide. Moreover, the algal diversity and cover was considerably greater; thus high-relief rocky reefs provided the most structurally diverse and persistent habitat.

Low-relief rocky reefs and sand/eelgrass were temporary habitats primarily utilized during the summer, coincident with summer vegetation growth. Presumably rockfishes utilize these habitats when structure and prey availability are highest and subsequently move to other more suitable habitats (Matthews In press). Although rockfish densities were low, these habitats cover considerably more area than artificial reefs or high-relief rocky reefs in Puget Sound, and thus are important to rockfish.

The highest densities of rockfishes were observed on the artificial reefs, primarily 80–200 mm quillback rockfish. Artificial reefs had high densities of 80–200 mm quillback rockfish throughout the year, although some fluctuations occurred, and high densities of large copper rockfish in the fall, winter, and spring. No other reefs surveyed had such high densities of 80–200 mm rockfishes of any species, and it is not known whether this results from higher survival of small quillback rockfish on artificial reefs. Furthermore, it is puzzling that more large quillback rockfish were not found on the artificial reefs, considering the abundance of 80–200 mm quillback rockfish. Several hypotheses could explain the low numbers of large quillback rockfish on the artificial reefs: (1) Artificial reefs are not suitable habitat for large quillback rockfish, i.e., they leave when they grow large; (2) the fish have not yet grown to the larger size; (3) some factor is preventing the fish from growing; or (4) there is a high mortality of fish once they reach the 200-mm size. I ruled out the possibility that large copper rockfish competitively excluded large quillbacks, as the two species coexist on high-relief natural reefs, although competition may be reduced at high-relief habitats if resources are not limiting. The shortage of large quillback rockfish on the artificial reefs is not depth-related since large quillbacks have been observed at similar depths in other studies (Moulton 1977, Richards 1987) and at HR1 and HR2. Again, the lack of large quillback rockfish was not due to fishing pressure: I observed low levels of fishing at both artificial reefs. Furthermore, if fishing pressure was responsible for the lack of large fish, there would be few large copper rockfish. In any case, this apparent refuge for 80–200 mm quillback rockfish should be investigated to determine if rockfish leave once they reach a certain size and eventually contribute to recreational fisheries. Although it has been well established that artificial reefs attract high densities of fish, in this case 80–200 mm quillback rockfish, there is no information that verifies whether there is adequate food or if growth or mortality is similar to that observed on natural reefs (Ambrose and Swarbrick 1989).

Year-to-year comparison

In a 4-year study of kelp-bed fishes in southern California, Ebeling et al. (1980) found little annual variation in numbers of bottom assemblages, including rockfishes. Although my study demonstrated significant seasonal changes within a habitat (artificial reefs, low relief, sand/eelgrass), when analyzed between seasons there were few differences between years, with the exception of YOY. Ebeling et al. (1980) suggested that the low annual variation in kelp-bed fish assemblages was characteristic of stable communities in predictable environments. Although more recent work (Ebeling and Laur 1988) demonstrated the dramatic effect storms can have on fish populations, Puget Sound is a relatively protected environment not subjected to open ocean waves and surge. Thus year-to-year variation in Puget Sound rockfish populations may be small.

Species comparison

Copper rockfish occurred on all habitats and can be considered a habitat generalist. Large copper rockfish were observed on all four habitats, although they left the artificial reefs in the summer and moved into shallower low-relief and sand/eelgrass areas. Buckley and Hueckel (1985) also noted a seasonal decrease of copper rockfish densities during the summer on Gedney Island artificial reef in central Puget Sound, and highest densities were noted during the fall and winter. They speculated rockfish movement was in response to prey occurrence (surfperch). Moulton (1977) speculated that copper rockfish move to deeper water during the fall in northern Puget Sound due to seasonal depth preference or prey availability. Turbulence presumably does not contribute to movement; in Puget Sound most water motion on the bottom is from currents, not surge or turbulence, and water motion is similar in the summer and winter. In the summer, copper rockfish utilized several habitats: high-relief rocky reefs, low-relief reefs, and sand/eelgrass. Their appearance on the shallower reefs during the summer and disappearance from the deeper artificial reefs is not simply a shallower depth preference in the summer; copper rockfish were observed during the summer at the high-relief reefs even at comparable artificial reef depths.

Quillback rockfish were more restricted in their distribution when compared with copper rockfish. Similarly, quillback rockfish were not as widely distributed as copper rockfish at 12 study sites in the Strait of Georgia (Richards 1987). The small quillback rockfish were seen in very high densities on the artificial reefs, but infrequently on other habitats. Large quillback rockfish were primarily seen on high-relief rocky and artificial

reefs; Richards (1987) noted quillback rockfish densities were correlated with relief, and highest densities were found on complex habitats. The lack of large quillback rockfish on low-relief and sand/eelgrass areas is presumably due to their preference for high relief and complex habitats.

Brown rockfish displayed the most restricted and perplexing distribution, primarily being found on Orchard Rocks high-relief reef and the inshore low-relief reefs during the summer, and rarely observed on artificial reefs or sand/eelgrass. Brown rockfish have been observed on artificial reefs in south Puget Sound (Greg Hueckel, Wash. Dep. Fish., Olympia, WA 98504, pers. commun., summer 1988) and it is unclear why they did not inhabit the artificial reefs in central Puget Sound. Additionally, brown rockfish are relatively uncommon on rocky reefs in northern Puget Sound and the San Juan Islands (Moulton 1977). In California, brown rockfish are primarily found on sandy, low-relief areas (Matthews 1985); their different habitat use in Puget Sound could be due to local hybridization with congeners (L. Seeb, Southern Ill. Univ., Carbondale, IL 62901, pers. commun., summer 1987).

YOY were distributed differentially among all habitat types. The sand/eelgrass was a temporary YOY habitat, as YOY were observed in July and never again seen. Either the YOY left the area or died. Similarly, YOY were observed on the low-relief reefs but subsequently emigrated or suffered high mortality; their contribution to recruitment on other reefs is unknown. On the other hand, YOY were first observed on the transects on HR2 in August, although they were previously seen in July off the reef on adjacent (within 25 m) sand/*Agarum*. The numbers of YOY increased over the next few months, peaked in November, and initial settlement was followed by an increase in the 80–200 mm copper, quillback, and brown rockfishes, presumably, the result of recruits staying and growing into the larger size category. A similar pattern of YOY influx was followed by an increase in the 80–200 mm group on AR2, although two periods of YOY settlement were observed, spring and fall.

Parturition of these rockfishes reportedly occurs April through June, as most female rockfishes captured April and May near Bainbridge Island had embryos and ovaries that were in the transitional stage during the summer (DeLacy et al. 1964, Washington et al. 1979, Dygert 1986). On SCUBA surveys, I saw pregnant rockfish late April through late June. Therefore, the YOY that were observed during the summer and fall of 1987 on HR2 presumably were released between April and July, spent some unknown amount of time in pelagic regions or on some other habitat, and then settled to a demersal existence in July and August. Examinations of the otolith microstructure of eight 45–60 mm TL rockfish (M. Yoklavich, Natl. Mar. Fish. Serv., Seattle, WA 98115, pers. commun., fall 1987) that I collected 29 August 1987 on HR2 revealed approximately 120–160 growth rings. Similar growth rings have been shown to be deposited daily in black rockfish (Yoklavich and Boehlert 1987). If the rings examined on my rockfish were also daily, it would confirm that parturition occurred around April. Additionally, these fish appeared to grow quite quickly. When first observed in July and August they were approximately 45–60 mm TL and by November were 90–100 mm TL (fish were captured to verify these measurements). This scenario describes the parturition on the natural reefs which was quite different from the YOY settlement on Boeing Creek artificial reef. YOY were assumed to be primarily quillback rockfish, as YOY settlement was followed by an increase of 80–200 mm quillback rockfish. They were observed in the spring and the fall on Boeing Creek artificial reef. It is unclear when the spring recruits were released or if there are possibly two reproductive periods for quillback rockfish in Washington as noted for some California rockfishes (Wyllie Echeverria 1987). Brown rockfish sampled from one location in north-central California had two distinct seasons of larval extrusion, December and June, and Wyllie Echeverria (1987) concluded that rockfishes have a flexible reproduction system that enables individuals to adaptively respond to environmental factors. On the other hand, in my study young quillback rockfish could arrive from another source—northern Puget Sound, Strait of Juan de Fuca, or even the outer coast of Washington—causing the second pulse.

On Vancouver Island, Haldorson and Richards (1987) noted an influx of YOY (<50 mm) copper rockfish during August and September; the YOY utilized four habitat types: (1) *Nereocystis leutkeana*, (2) *Agarum* slopes, (3) eelgrass, and (4) sand. They observed the highest densities of young copper rockfish first in the bullkelp canopies. Subsequently, the young rockfish left the kelp canopy and were found on the floor of the kelp forest in September and October, coincident with fall storms and the annual decomposition of the bullkelp. After the initial association with the kelp canopy, the YOY shifted their distribution to a demersal habitat with the perennial macrophytes *Agarum* and eelgrass. Similarly, Carr (1983) first observed YOY copper rockfish in the upper canopy of giant kelp *Macrocystis pyrifera* in central California kelp beds. The YOY copper rockfish subsequently moved toward the bottom over the following weeks. Carr (1983) and Haldorson and Richards (1987) always observed YOY in close proximity to drift or attached kelp or eelgrass and suggested that young rockfishes strongly associated with plant cover to avoid predation and find food resources.

Interestingly, I never observed YOY in bullkelp canopy. The young fish were only seen on the bottom closely associated with the perennial understory macrophytes *Agarum*, *Pterygophora*, and eelgrass, or closely associated with rocks at AR2, which has little plant cover. The YOY could have spent a short period of time in the bullkelp canopy before I first saw them in my surveys or they may never use the bullkelp canopy in my study sites. Young rockfish may not be able to maintain position in the water column in areas with current.

It is not surprising that YOY rockfishes were seen in 1987, yet not in 1988. The numbers of first-year rockfish recruits reportedly vary greatly year-to-year along the coast of central and northern California (Hobson et al. 1986, Gaines and Roughgarden 1987). Studies in California have documented wide fluctuations in YOY recruitment sometimes influenced by warm-water years and changes in distribution after kelp removal (Bodkin 1988). Temperature did not appear to be a factor in the absence of YOY in 1988; bottom temperatures were similar between 1987 and 1988 (Fig. 8). In addition, few YOY were observed off eastern Vancouver Island during the same time period (summer and fall 1988) (L. Richards, Pac. Biol. Sttn., Nanaimo, B.C., Canada V9R 5K6, pers. commun., spring 1989). Apparently, copper, quillback, and brown rockfish recruitment is episodic; this has important implications to our understanding of the population dynamics and management of Puget Sound rockfishes.

The most numerous aggregations of YOY were observed on low-current reefs: HR2, AR2, and SE2. YOY were never observed on the highest current reefs, HR1 and AR1. Possibly YOY settle out on high-current reefs but lack the ability to remain on the reef and are swept away by strong current. In contrast, larvae may accumulate at sites of low current velocity. Leaman (1976) collected significantly higher numbers of *Sebastes* larvae in sheltered waters than in open, more exposed channels off the west coast of Vancouver Island. Similarly, Haldorson and Richards' (1987) observations of YOY rockfishes on eastern Vancouver Island were in low-current areas.

Experimental design

Because underwater transects are an effective means of describing large diurnally active fish populations (Brock 1954, Brock 1982), my transects were probably effective for estimating abundances of adult rockfishes, although I probably underestimated YOY rockfishes and the very dense aggregations of 80–200 mm quillback rockfish on the artificial reefs. For many size categories of the three species during most seasons, there were density differences between the two replicate sites (reefs) within each habitat type. This variability suggests there may not be a typical rocky reef or artificial reef. In most cases, though, this difference was due to variability in densities and not to different species present on the reef. For example, both AR1 and AR2 had very high densities of 80–200 mm quillback rockfish, perhaps a characteristic of artificial reefs in Puget Sound. High densities of 80–200 mm rockfishes were not observed on any other reef type, but AR2 had significantly larger densities, perhaps due to location or age of the reef.

Habitat quality

Which is the highest quality habitat? One view of habitat quality would predict that densities are directly proportional to quality; rockfish densities are highest where habitat quality is highest. This reasoning forms the basis of many current habitat assessment models in resource management (Van Horne 1983). In the absence of long-term information on growth, survival, stability, and other features of how species respond to different habitats, habitat quality is evaluated in short-term studies describing densities (Van Horne 1983). Those habitats with the highest densities will be those most important to the maintenance of that species and should ultimately be protected as critical habitat. It is important to note that densities can be misleading in designating habitat quality (Van Horne 1983). While my habitat surveys documented the highest rockfish densities on artificial reefs, the densities underwent major fluctuations. According to classic ecological theory, as density increases habitat quality declines (Svardson 1949, Fretwell 1972). If resources are limited, then at high rockfish densities, food, hiding, and resting places would be in short supply, thereby reducing growth and survival. In my study, changes in availability of resources presumably were the causes for rockfish density fluctuations. Therefore, a true measure of habitat quality should include factors other than densities, such as availability of essential resources, stability over time, survival, reproductive output, growth, and the animal's preference for that habitat. Nevertheless, copper, quillback, and brown rockfish utilized all four habitat types surveyed, and each habitat is important. But some of these habitats vary seasonally vary their suitability, and so rockfishes move to exploit alternate habitats when suitability is low (Matthews In press). Thus, for rockfishes, I would argue that high densities should not be the primary indicator of habitat quality, particularly in reference to the high ratio of small/large quillback rockfish on artificial reefs. Documenting densities of rockfishes only during a short time frame (few months) would not be representative of that habitat's importance. In addition, low-relief rocky reefs, although only important as

rockfish habitat in the summer, likely represent essential summer feeding area for rockfishes. Although densities are low, this habitat type is widespread in Puget Sound. In order to protect low-relief habitats, they would obviously have to be preserved year-round, i.e.. not altered or destroyed. Thus, in terms of seasonal stability in densities, presence of all size categories, and seasonal resource availability, I suggest the following ranks for the different habitats, listed from highest to lowest: High-relief rocky reefs, low-relief reefs (important as summer feeding area and thus contribute to year-round growth), artificial reefs (pending further research and assessment), and sand/eelgrass.

Regardless of which habitat has the highest quality, the habitat types examined in this study were utilized differently by the various size groups and species. Recently, however, Hueckel et al. (1989) have suggested that artificial reefs can be used as mitigation for the loss of natural rocky-reef habitat. Mitigating the loss of natural habitats with artificial reefs uses the rationale that artificial reefs provide rocky-reef type substrate that replicates natural rocky reefs. Hueckel and Buckley (1989) reported that artificial reefs in Puget Sound replicate processes on natural reefs and provide as evidence the similarity in the number of fish and prey species present on artificial and natural reefs. My research indicated that rockfish species composition was similar (with the exception of brown rockfish) between natural and artificial reefs. However, these species utilize artificial reefs quite differently than natural reefs: Large copper rockfish leave artificial reefs during the summer, large quillback rockfish are found in small numbers, and artificial reefs are dominated by extremely high densities of small quillback rockfish, unlike any natural reef I surveyed. In fact, the artificial reefs I studied seem to represent an anomalous habitat unlike any natural habitat.

Furthermore, the difference in resource availability and habitat use may result in different birth and death rates on different habitats. Thus, the different habitats could be viewed as sources, where reproductive output exceeds deaths, or sinks, where a deficit exists (Pulliam 1988). On the superficial observation of high densities of quillback rockfishes on artificial reefs, it could be determined that the destruction of a nearby rocky reef would have little impact on rockfishes. Pulliam (1988) points out that if a habitat (e.g., artificial reef) being preserved was a sink and the one being destroyed was a source (e.g., natural rocky reef), destruction of a relatively small source habitat could then have disastrous results. For example, if a low-relief natural reef was destroyed for a development project, the loss of the productive feeding area used by artificial-reef rockfishes during the summer could result in reduced growth and less reproductive output. Again, whether or not artificial reefs provide adequate food for such high densities of rockfishes is unknown. The largest rockfish inhabiting artificial reefs were those that made use of natural habitats; their movement was confirmed in a tagging study (Matthews 1988). Thus copper rockfish may be maintained by a source habitat when they make use of kelp beds during the summer. In addition, artificial reefs are considerably smaller than natural reefs, so they would not compensate for the total loss of abundance (Ambrose and Swarbrick 1989). Thus it is premature and speculative to suggest that artificial reefs should be used as mitigation.

Summary

Habitat surveys comparing monthly densities of copper, quillback, and brown rockfishes on high-relief rocky reefs, low-relief rocky reefs, high-relief artificial reefs, and sand/eelgrass areas demonstrated strong differences in how rockfishes utilize these habitats. High-relief rocky reefs had the most consistent densities of the three species of rockfishes, mostly fish >200 mm. Low-relief rocky reefs were primarily inhabited in the summer months coincident with the summer growth of *Nereocystis leutkeana*. YOY rockfishes were also observed on low-relief reefs; however, most fish left these reefs in the fall. The highest densities of rockfishes, primarily 80–200 mm quillback rockfish (up to 420/90-m^3 transect), were observed on artificial reefs and high densities of large copper rockfish were also observed. On artificial reefs, density fluctuations were dramatic; copper rockfish densities peaked in the fall and winter and declined (to 0/transect) during the summer and quillback rockfish densities also seasonally fluctuated. Brown rockfish were rarely seen on the artificial reefs. Sand/eelgrass areas were the least utilized habitat type; only during July and August were YOY, adult copper rockfish, and brown rockfish observed on one sand/eelgrass habitat. Although all four habitats were used, natural reefs may represent source habitats that are used by and maintain rockfishes on less productive sink (artificial reef) habitats. Thus the recent use of artificial reefs as mitigation for the loss of natural reefs could have negative impacts on rockfish populations.

Acknowledgments

I am grateful to the many people who helped me complete this study, which was part of my dissertation research at the University of Washington School of Fisheries. I was fortunate to have the expert diving assistance of Robert Reavis throughout the entire

course of my field work; other divers included Vince Macurdy, Wayne Palsson, and Tony Unthank. Dr. Loveday Conquest and Kevin Lohman assisted me with statistical consultation. Funds for this project were provided by the Federal Aid to Sport Fish Restoration Act (Wallop-Breaux), Project F-81-R; Segments 1-3, Monitoring and Assessment of Puget Sound Recreational Bottomfish Stocks, through the efforts of Greg Bargmann, Cyreis Schmitt, and Wayne Palsson at Washington Department of Fisheries. Support during manuscript preparation was provided by a Canadian Government Postdoctoral Fellowship at the Pacific Biological Station. This manuscript was greatly improved by constructive reviews from Greg Bargmann, Dee Boersma, Mark Carr, Don Gunderson, Bruce Miller, Wayne Palsson, Tom Quinn, Cyreis Schmitt, and two anonymous reviewers.

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Separation of Two Species of Sand Lances, *Ammodytes americanus* and *A. dubius*, in the Western North Atlantic

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Abstract.—Two species of sand lances are recognized in the western North Atlantic, the inshore *Ammodytes americanus* DeKay 1842 and the offshore *A. dubius* Reinhardt 1838. The best separation of the two species is achieved by using the number of plicae (oblique folds of skin on the lateral body surface) singly or in combination with the number of vertebrae. *Ammodytes americanus* has fewer meristic structures than *A. dubius*: number of lateral plicae 106–126, $\bar{x}$ 117.4 vs. 124–147, 132.1; total vertebrae 62–70, $\bar{x}$ 66.4 vs. 68–76, 70.8; dorsal fin rays 52–61, $\bar{x}$ 57.4 vs. 56–67, 61.8; anal fin rays 26–33, $\bar{x}$ 29.4 vs. 28–35, 31.1; pectoral fin rays 11–15, $\bar{x}$ 13.2 vs. 12–16, 14.0; gill rakers on first arch 21–28, $\bar{x}$ 24.3 vs. 23–31, 26.6. Meristic differences between species were summarized with principle component analysis. In addition to considerable variation within samples, there is geographic variation in numbers of vertebrae, plicae, and dorsal and anal fin rays, particularly in the offshore *A. dubius*. Specimens from the Scotian Shelf north have higher counts than do specimens from more southern populations. Based on specimens examined, *A. americanus* occurs from southern Delaware north to Labrador in shallow coastal waters as well as in protected bays and estuaries. *Ammodytes dubius* is found in deeper, open waters from North Carolina to Greenland.

Manuscript accepted 26 January 1990.
Fishery Bulletin, U.S. 88:241–255.

Members of the genus *Ammodytes*, or sand lances, are small elongate fishes abundant over shallow, sandy areas of the continental shelves of northern oceans. They are important prey items for several commercial fishes (e.g., American plaice, cod, haddock, silver hake, yellowtail flounder, and Atlantic salmon (Reay 1970, Meyer et al. 1979, Winters 1983) as well as fin and humpback whales (Overholtz and Nicolas 1979) and various kinds of seabirds (Reay 1970, Powers and Backus 1987). Additionally, in the North Sea and off Japan, sand lances are the basis for an important fish-meal industry (Macer 1966).

Western North Atlantic populations of sand lances have increased dramatically in recent years (Sherman et al. 1981, Winters 1983). This population explosion was correlated with a decline in stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* along the eastern coast of the United States (Population Dynamics Branch, Conservation and Utilization Div., Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA 02543) (Fig. 1). The opportunistic sand lances seemed to have replaced these stocks. Concurrently, piscivorous fishes increased their consumption of sand lances. Peak abundance of sand lances in this region was reached in 1981, and numbers have since decreased (Nelson and Ross 1987). Again, the shift in sand lance abundance was correlated with mackerel numbers; mackerel populations have been steadily increasing since 1983 (Fig. 1). In view of the ecological importance and population dynamics of sand lances, it is important that the taxonomic status of these fishes be resolved.

Although the taxonomy of the majority of fish species in the western North Atlantic Ocean is known reasonably well, *Ammodytes* is a major exception despite the results of several detailed studies (e.g., Richards et al. 1963, Scott 1972, Winters and Dalley 1988). Recognition of two species of *Ammodytes* in the western North Atlantic dates back to at least Jordan and Evermann (1896). Since then, the majority of researchers have fundamentally accepted this finding (Bruun 1941, Backus 1957, Richards et al. 1963, Leim and Scott 1966, Winters 1970, Scott 1972, Winters and Dalley 1988, Scott and Scott 1988). However, final conclusions on species names, synonomies, and meristic and geographic ranges vary between studies. *Ammodytes americanus* DeKay 1842 and *A. dubius* Reinhardt 1838 are currently accepted as the appropriate names for these sand lances (Leim and Scott 1966, Reay 1970, Richards 1982, Winters and Dalley 1988), and until a worldwide systematic revision

of the family is completed these names should be used.

Taxonomic confusion results mainly from the morphological similarity and large variability in characters traditionally used to separate and identify the different species of *Ammodytes*. Generally, distinguishing characters have been limited to meristic ones, especially numbers of vertebrae and dorsal and anal fin rays. Meristic overlap and variability are further complicated by the trend for more northerly populations of both species to have higher counts. Meristic characters show clinal variation, increasing both with latitude and distance offshore (Richards et al. 1963, Scott 1972, Richards 1982). Body depth and maximum total length have also been used to separate species (Richards et al. 1963, Winters and Dalley 1988), although this character combination has been shown to vary greatly with stage of maturity and age. In fact, intraspecific variation is greater than interspecific variation in some cases (Scott 1972). Additionally, the phase of the reproductive cycle and the amount of food present in the digestive tract also affect body depth in these fish.

With numerous hypotheses and species names circulating in the literature (see Richards et al. 1963 and Winters and Dalley 1988 for additional reviews), a need to alleviate some of the confusion associated with this genus is obvious. The western North Atlantic sand lances were studied in detail to determine appropriate species definitions, delimit geographic distributions, and describe meristic variation.

Historical background

Systematic problems involving *Ammodytes* are prevalent at all levels of taxonomic complexity. Researchers still are not sure of the phylogenetic relationships between genera of sand lances and the systematic placement of the Ammodytidae among perciforms. Pietsch and Zabetian (1990), however, believe ammodytids to be trachinoids with the family Ammodytidae the sister group of the Trachinidae plus Uranoscopidae.

At the alpha taxonomy level, 23 nominal species of the genus *Ammodytes* have been described. However, only the following six species have been consistently recognized in the literature: *A. americanus* DeKay 1842 and *A. dubius* Reinhardt 1838 in the western North Atlantic, *A. marinus* Raitt 1934 and *A. tobianus* Linnaeus 1758 in the eastern North Atlantic, and *A. hexapterus* Pallas 1811 and *A. personatus* Girard 1857 in the North Pacific (Reay 1970). However, Reay's (1970) synopsis of valid species names and delimitations of geographic ranges has not always been accepted; synonymies and geographical range adjustments are abundant. For instance, several workers including

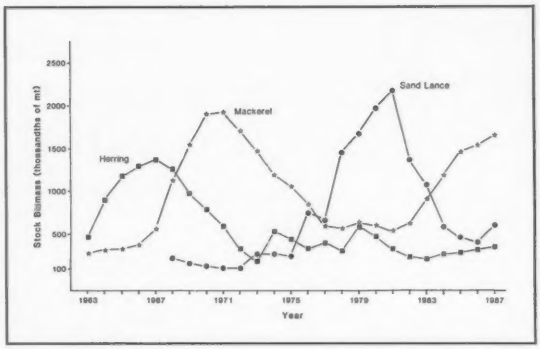

Figure 1

Abundance (10^6 metric tons) of mackerel *Scomber scombrus*, herring *Clupea harengus*, and sand lance *Ammodytes dubius* populations, 1963–87, in the western North Atlantic (Northeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Woods Hole, MA).

Andriashev (1954), Walters (1955), McAllister (1960), and Richards et al. (1963) have proposed that *A. hexapterus* is circumpolar and synonymous with *A. americanus* and/or *A. marinus*. Regarding the sand lances that occur in the extreme northern oceans (particularly Greenland), some investigators suggest that the low-count inshore form should be regarded as *A. americanus* (Reay 1970). Winters and Dalley (1988) proposed that these northern populations were *A. marinus*. Thus, these two nominal species may be conspecific, but researchers disagree on which name to use for the species in the western North Atlantic. *Ammodytes dubius* also occurs off the coast of Greenland but generally is considered to be a distinct species (e.g., Backus 1957, Reay 1970, Winters and Dalley 1988). Additionally, Jensen (1941, 1944) suggested that the broad overlap in characters used to separate *Ammodytes* species is so great that there may be only one extremely variable, polymorphic Atlantic species of sand lance.

Furthermore, clinal variation adds to the taxonomic confusion since some investigators recognize this variation as worthy of species designation while others propose the use of subspecies or only recognize isolated populations. Richards et al. (1963) suggested that clinal variation may be due to effects of environmental factors such as temperature, a phenomenon that has been documented in many other marine fishes. These trends have been reported in all species of *Ammodytes*, again leading to the suggestion of a single heterogeneous species with meristic and morphological differences attributable to environmental variables related to distribution.

Methods

Approximately 1500 specimens from a range of locations (North Carolina to Greenland) along the western North Atlantic coast were examined in this study (Fig. 2; Appendix 1). Total number of gill rakers were counted on the first arch on the right side; pectoral fin rays were counted on the left. Dorsal and anal ray counts were obtained from radiographs. The anterior 1–3 pterygiophores of the dorsal fin may have no associated fin ray; therefore, dorsal fin counts began at the first visible ray. Several cleared and stained specimens were examined to verify counts obtained from radiographs. Precaudal, caudal, and total vertebral counts were also taken from radiographs. The first caudal vertebra was defined as the centrum bearing the first elongate hemal spine. Total vertebral counts exclude the hypural plate following the practice of most recent workers on the genus.

Sand lances possess distinctive rows of oblique folds of skin or plicae which occur on the lateral body surfaces and are lined on the undersides by cycloid scales. The rows of plicae characteristically extend from an area above the pectoral fin base to the caudal peduncle. Plicae length and the angle of direction at which plicae run are highly variable near the head and tail (Fig. 3). Total plicae counts proved difficult to make and were not repeatable. Therefore, we modified plicae counts to begin with the first plica posterior to the first

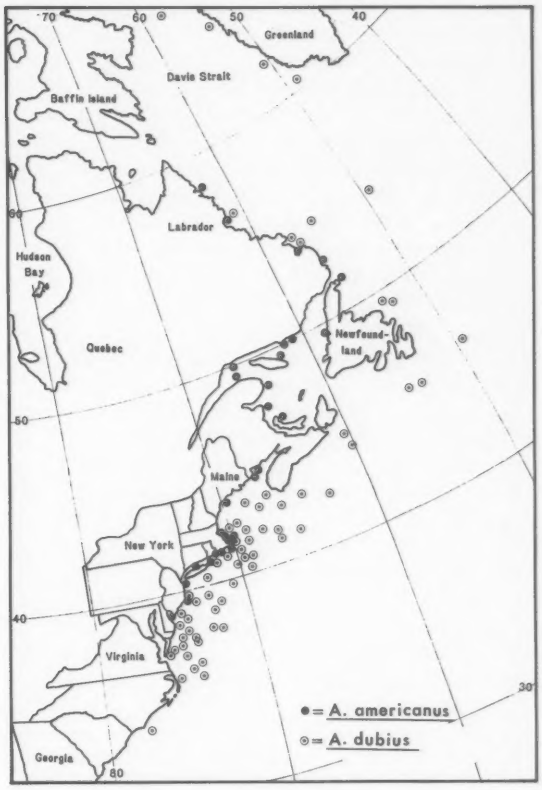

Figure 2

Distribution of *Ammodytes americanus* and *A. dubius* in western North Atlantic based on specimens examined for this study.

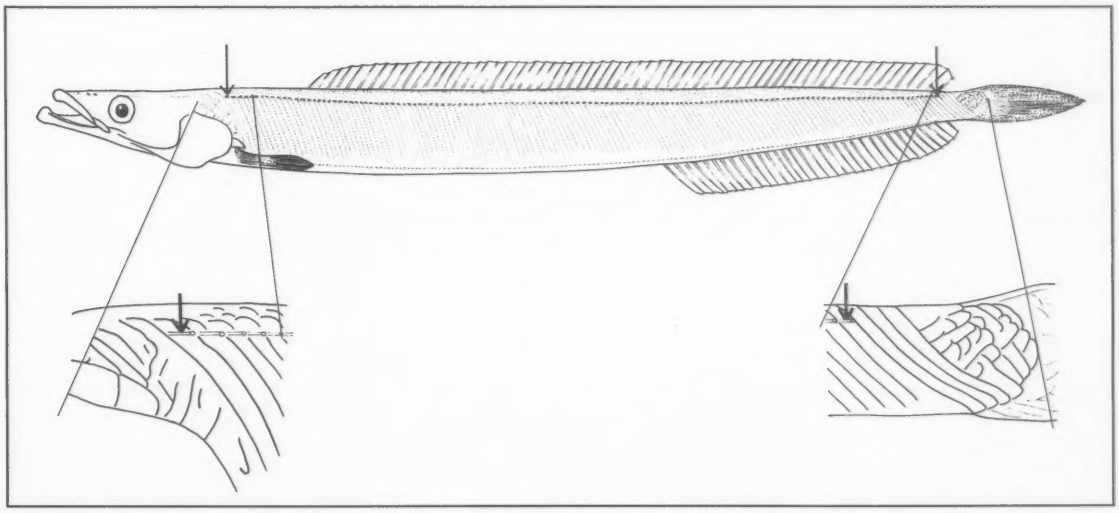

Figure 3

Drawing of *Ammodytes dubius* shows how plicae were counted (between arrows). The irregular plicae present anteriorly and posteriorly (see insets) were not counted.

pored lateral line scale and continuing posteriorly to the plica associated with the last pored scale (Fig. 3). Because plicae are much easier to count than scales, the folds themselves were counted between the two end points. If, however, the regular serial arrangement of plicae was interrupted (i.e., size and direction of slope of the plicae become irregular), the pored lateral line scales were counted in order to maintain consistency in counts between specimens. Plicae counts made in this manner are much more consistent.

Meristic data were divided into four geographic regions in order to describe and analyze geographic variation: Labrador, Quebec–Nova Scotia, Maine–Massachusetts, and New York–North Carolina. Since three species of *Ammodytes* may be present in Greenland waters, Greenland specimens were analyzed separately. Conclusions made with regard to the other geographic regions were applied to Greenland collections in an effort to determine which species are present in this region.

To determine if two species could be distinguished objectively, principle component analysis (PCA) was conducted on a covariance matrix for meristic characters (plicae, vertebrae, dorsal, anal, and pectoral fin rays, and gill rakers) for 332 individuals. These specimens, all with a complete complement of meristic values, were pooled from locations throughout the geographic range, exclusive of Greenland. An attempt was made to give equal representation to each area; however, there were not many offshore collections from Labrador available. Since the data set contained both individuals with low meristics and those with high counts, the assumption was made that both forms were present within the sample. An individual's score on the first component was determined by entering its values for meristic characters into an equation. Component scores were plotted and two groups are clearly present (Fig. 4). The point of least overlap was chosen as the boundary between the two species. Data points were then coded using earlier tentative identifications (based on observed meristic trends) to determine the effectiveness of the methodology. The equation and the value of the score at the boundary between the two species were cross-validated by testing an additional 54 specimens.

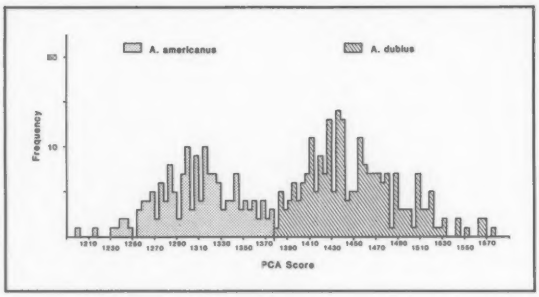

Figure 4

Histogram of principal component analysis (PCA) scores for six meristic characters of *Ammodytes*. Ranges: *A. americanus* 1199–1378, *A. dubius* 1378–1572. Component scores were calculated using the following equation: (8.09 × number of plicae) + (2.44 × number of dorsal rays) + (2.31 × total number of vertebrae) + (1.23 × total number of gill rakers) + (1.03 × number of anal rays) + (0.45 × number of pectoral rays).

Results

Number of lateral plicae was the most useful single character in separating the two species, even though plicae numbers varied considerably between individuals and slightly from side to side in individual specimens (Table 1). Of 723 specimens included in the analysis, 98.8% could be separated into species at a line of separation between 124 and 125 plicae (Fig. 5). *Ammodytes americanus* had fewer plicae, ranging from 106 to 126 ($\bar{x}$ 117.4) with virtually no geographic variation; *A. dubius* had more plicae (124–147, $\bar{x}$ 132.1) and exhibited geographic variation. Plicae means for *A. dubius* ranged from 131.2 in the New York–North Carolina region to approximately 132–136 from Massachusetts northward.

Number of vertebrae, a standard character examined by previous researchers interested in *Ammodytes*, also proved to be a relatively good character in separating species. Although some overlap in vertebral numbers exists, particularly south of Nova Scotia, 92.3% separation was achieved at a line of separation between 68 and 69 vertebrae (Table 2). *Ammodytes americanus* had fewer vertebrae, with mean values ranging from 65.2 in specimens from New York to North Carolina and increasing to a mean value of 67.2 in specimens from Quebec to Labrador. *Ammodytes dubius* characteristically had more vertebrae than *A. americanus*, with means ranging between 70–71 in the southern portions of its range (Maine to North Carolina) to 73.8 in the Quebec–Nova Scotia region and 71.9 off Labrador. There is a distinct increase in vertebral number ($\bar{x}$ 72.9) in specimens of *A. dubius* taken off the Scotian Shelf and northward.

Dorsal ray counts were also effective in separating specimens. Using this character alone, 92.3% of the specimens could be separated at a line of separation between 59 and 60 dorsal rays. *Ammodytes americanus* had relatively consistent dorsal ray counts throughout the entire geographic range (Table 3; 52–61, $\bar{x}$ 57.4); however, in comparison, number of dorsal rays for *A. dubius* was higher for specimens collected north of

Table 1

Frequency distribution of plicae counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
106			1		1					
107			1		1					
108	1		1		2					
109	1		—	1	2					
110	1	1	1	2	5					
111	2	5	—	1	8					
112	5	1	7	3	16					
113	2	2	1	8	13					
114	5	4	8	16	33					
115	7	4	7	7	25					
116	10	4	3	11	28					
117	10	7	8	10	35					
118	18	9	5	12	44					
119	13	2	6	6	27					
120	8	2	6	5	21					
121	8	9	6	5	28					
122	8	3	6	2	19					
123	1	2	4	7	14					
124	1	2	8	5	16	1		2	2	5
125	1			2	3	3	1	—	8	12
126	1				1	2	—	2	10	14
127						4	—	2	25	31
128						1	—	3	14	18
129						1	3	4	24	32
130						2	2	8	33	45
131						1	2	6	20	29
132						2	3	9	18	32
133						—	1	1	22	24
134						1	6	8	23	38
135						1	2	2	19	24
136						—	3	3	9	15
137						1	8	3	6	18
138						—	4	4	5	13
139						4	4	1	3	12
140						1	2	2	1	6
141						—	2	—	—	2
142						—	—	—	—	—
143						2	3	—	1	6
144							1	1	1	3
145							1	—		1
146								—		—
147								1		1
$\bar{x}$	117.6	117.4	117.7	116.1	117.4	131.8	136.0	132.6	131.2	132.1
N	103	57	79	103	342	27	48	62	244	381

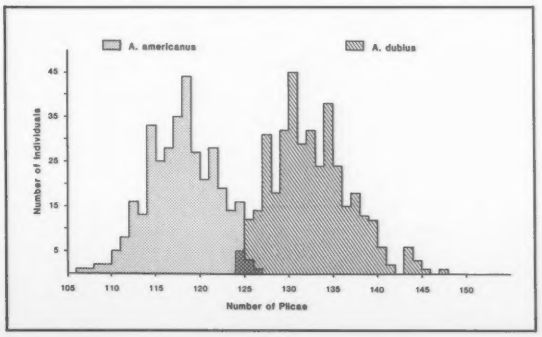

Figure 5

Histogram of counts of lateral plicae for *Ammodytes americanus* (106–126, $\bar{x}$ 117.4) and *A. dubius* (124–147, $\bar{x}$ 132.1).

Table 2
Frequency distribution of vertebral counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
62				2	2					
63	1			8	9					
64	6	1	11	18	36					
65	4	3	9	40	56					
66	17	8	14	16	55					
67	24	21	16	7	68					
68	29	16	18	3	66	2			16	18
69	15	4	7	4	30	3		12	39	54
70	1	1	2	1	5	5		23	87	115
71						3	1	22	64	90
72						2	3	3	23	31
73						2	15	1	4	22
74						6	14			20
75						4	8			12
76							3			3
$\bar{x}$	67.2	67.2	66.6	65.2	66.4	71.9	73.8	70.3	70.2	70.8
N	97	54	77	99	327	27	44	61	233	365

Table 3
Frequency distribution of dorsal ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
52			1		1					
53	1		2	1	4					
54	1	2	3	2	8					
55	1	4	5	7	17					
56	12	5	9	7	33				1	1
57	15	16	8	8	47				—	—
58	21	10	8	5	44	1		1	2	4
59	19	10	8	2	39	4		1	11	16
60	12		3	2	17	2		3	35	40
61	1		1	3	5	1		12	77	90
62						3	2	19	80	104
63						1	7	6	23	37
64						2	14		6	24
65						2	11			13
66						3	6			9
67						1	2			3
$\bar{x}$	57.9	57.2	56.9	56.9	57.4	62.4	64.4	61.5	61.3	61.8
N	83	47	48	37	215	20	42	42	235	341

Maine. Overall, dorsal ray counts for *A. dubius* varied from 56 to 67 rays. Specimens examined had means of 62.4 and 64.4 for Labrador and Quebec–Nova Scotia, respectively, compared with 61.5 in Maine–Massachusetts and 61.2 in the New York–North Carolina region.

Anal rays, the least successful character for separating specimens (Table 4), provided only 75.7% separation of individuals (at a line of separation between 29 and 30 anal rays). Means for *A. americanus* ranged from 29 in southern regions to 29.7 off the coast of Quebec northward to Labrador, with total number of rays varying between 26 and 33 (overall $\bar{x}$ 29.4). Geographic variation was again evident in anal ray counts for *A. dubius*. Counts averaged between 30 and 31 rays

Table 4
Frequency distribution of anal ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
26			2		2					
27	4	2	6	6	18					
28	10	4	15	3	32				4	4
29	23	13	8	15	59			1	27	28
30	27	18	8	9	62	2		17	76	95
31	13	9	7	4	33	6	2	15	99	122
32	6	2	3		11	6	6	11	32	55
33	1				1	4	17		5	26
34						3	14			17
35						1	7			8
$\bar{x}$	29.7	29.7	29.0	29.1	29.4	32.1	33.4	30.8	30.6	31.1
N	84	48	49	37	218	22	46	44	243	355

Table 5
Frequency distribution of pectoral ray counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
11			1		1					
12	12	5	14	10	41	1			4	5
13	62	40	49	53	204	17	2	10	35	64
14	20	11	14	35	80	6	25	39	155	255
15	1	1	1	5	8	3	21	14	47	85
16									2	2
$\bar{x}$	13.1	13.1	13.0	13.3	13.2	13.4	14.4	14.1	14.0	14.0
N	95	57	79	103	334	27	48	63	243	381

for specimens collected south of the Scotian Shelf (New York–North Carolina, $\bar{x}$ 30.6; Maine–Massachusetts, $\bar{x}$ 30.8) while specimens collected further north had mean values of 33.4 (Quebec–Nova Scotia) and 32.1 (Labrador).

The number of pectoral rays varied little geographically (Table 5) and was one of the least successful characters for separating the species. Modally, *A. americanus* had 13 rays (11–15, $\bar{x}$ 13.2) while *A. dubius* had one more ray, 14 (12–16, $\bar{x}$ 14.0). Only 78.0% of the specimens could be separated solely on this character (at a line of separation between 13 and 14 pectoral rays).

Gill rakers did not show pronounced geographic trends as was evident for vertebral counts (Table 6). For *A. americanus*, counts varied between 21 and 28, with means ranging from 23.7 (Labrador) to 24.9 (Massachusetts–Maine). Mean values for *A. dubius* clustered around 26 or 27 gill rakers ($\bar{x}$ 26.6, range 23–31 overall). At a line of separation between 25 and 26 gill rakers, 81.4% of the specimens could be separated into species using only this character.

Ammodytes dubius showed geographic variation in all the meristic characters examined. Meristic values increased northward with the exception of Labrador. Offshore Labrador collections were sparse; therefore, sample size is only half as large as other regions. Examination of additional material is necessary to determine if meristic values for *A. dubius* collected off Labrador are consistently lower.

The meristic characters used in this study separate the western North Atlantic sand lances into low- and high-count species. Each character, however, exhibited some overlap (ranging from approximately 3% for plicae counts to 49% for anal rays) and did not separate 100% of the specimens. Combinations of characters then became important in verifying identifications, particularly for individuals with intermediate counts.

Table 6
Frequency distribution of gill raker counts for *Ammodytes americanus* and *A. dubius* in four geographic regions.

	A. americanus					*A. dubius*				
	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total	Labrador	Quebec–Nova Scotia	Maine–Massachusetts	New York–N. Carolina	Total
21	1				1					
22	9	5	1		15					
23	30	18	7	13	68	4		1		5
24	28	22	19	29	98	5	1	4	7	17
25	18	7	23	22	70	4	3	8	37	52
26	2	5	14	15	36	4	9	18	70	101
27			5	5	10	4	10	7	66	87
28			1	1	2	2	13	6	50	71
29							7	—	9	16
30							1	1	3	5
31							2			2
$\bar{x}$	23.7	23.8	24.9	24.7	24.3	25.2	27.4	26.1	26.6	26.6
N	88	57	70	85	300	23	46	45	242	356

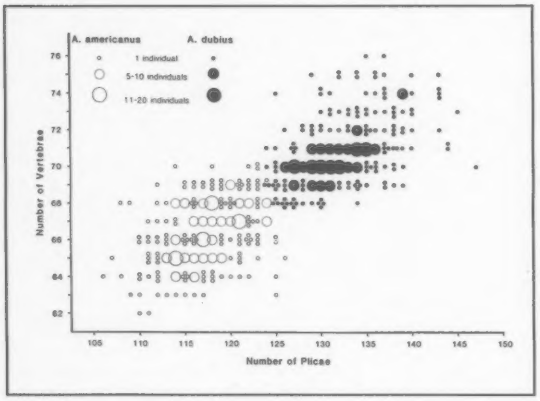

Figure 6
Scattergram of vertebral count plotted against number of lateral plicae for *Ammodytes americanus* and *A. dubius*.

Plicae and vertebral counts, when plotted against one another, were the most useful combination of characters for the entire geographic range producing virtually 100% separation (Fig. 6).

The results of a PCA run on meristic data confirmed the usefulness of these characters. Since factor 1 accounted for 91% of the variation and all the meristic characters loaded heavily on this factor, factor 1 was the only factor used. Plicae had the highest component loading score (8.09) followed by dorsal rays (2.44), vertebrae (2.31), gill rakers (1.23), anal rays (1.03), and pectoral rays (0.45).

The histogram of component scores (Fig. 4) produced a bimodal distribution with little overlap above or below a score of 1378 for the first set of individuals evaluated. When the scores were compared with the earlier tentative identifications (based only on meristics), only 10 (5 of each species) were either borderline or placed into the wrong species grouping. These 10 individuals were then reexamined and either the proposed identification was verified (3 cases) or errors in the counts of certain meristic characters were found (7 cases).

At most, 2% of the specimens were misclassified using the component scores. Of 54 additional specimens tested against the equation, none were misclassified. This methodology, therefore, was consistent and reliable.

Based on these results, diagnoses for the two species follow:

Ammodytes americanus

Diagnosis *Ammodytes americanus* tends to have lower counts than *A. dubius*: lateral plicae 106–126 ($\bar{x}$ 117.4); vertebrae 62–70, usually 64–69 ($\bar{x}$ 66.4); dorsal fin rays 52–61 ($\bar{x}$ 57.4), anal fin rays 26–33 ($\bar{x}$ 29.4), and pectoral fin rays 11–15 ($\bar{x}$ 13.2), with the most common dorsal, anal, and pectoral ray counts being 55–59, 27–31, and 13 rays, respectively; gill rakers on the first arch 21–28 ($\bar{x}$ 24.3).

Six meristic characters in combination provide a good separation of this species from *A. dubius*. Number of plicae, however, is the single best character for distinguishing *A. americanus* from *A. dubius* in the western North Atlantic. Vertebrae plotted against plicae separate individuals of the two species with little overlap (Fig. 6).

Distribution Based on our samples, *A. americanus* ranges coastally from southern Delaware north through

Labrador (Fig. 2). Previous studies reported its occurrence in Chesapeake Bay (Richards 1982, Norcross et al. 1961); however, no specimens were examined from Chesapeake Bay during this study.

This species occurs in shallow coastal waters and in protected bays and estuaries. Frequently, specimens were collected with seines or dipnets on sandy beaches in less than 2 m of water. Identification of individuals based only on locality (i.e., inshore vs. offshore) can be made with discretion, but some collections (approximately 20%), mainly from inshore stations, contain both species.

Ammodytes dubius

Diagnosis *Ammodytes dubius* shows geographic variation in meristic features (Tables 1–6), and counts for this species are higher than those of *A. americanus*: lateral plicae 124–147 ($\bar{x}$ 132.1); vertebrae 68–76 ($\bar{x}$ 70.8) with 69–74 being the most common; dorsal fin rays 56–67 ($\bar{x}$ 61.8), anal fin rays 28–35 ($\bar{x}$ 31.1), and pectoral fin rays 12–16 ($\bar{x}$ 14.0). The majority of individuals examined have ≥60 dorsal, ≥29 anal, and 14 pectoral rays. More gill rakers (23–31, $\bar{x}$ 26.6) are present on the first arch than in *A. americanus*. As described previously, plicae count is the best single distinguishing character; however, vertebrae plotted against plicae separate the species with little overlap (Fig. 6).

Distribution *Ammodytes dubius* ranges from North Carolina to Greenland (Fig. 2) and is found in deeper, more offshore waters than *A. americanus*. *Ammodytes dubius* is occasionally found inshore but is generally taken in deeper, open waters. This species has a broad bathymetric distribution in coastal waters and ranges in depth from 7 to 80 m. Both species were taken together in approximately 20% of the samples examined, with the majority of these samples being collected at inshore stations or around islands just offshore. Winters and Dalley (1988) reported co-occurrence inshore of *A. americanus* and *A. dubius*, particularly in Newfoundland waters. Although none of the collections that we examined from Quebec–Nova Scotia contained both species, mixed collections were found in all other geographic areas. Several mixed collections (6 of 11 collections) contained only one or two individuals of *A. dubius*, with the remainder of the lot being *A. americanus*. Two of the 11 collections were all *A. dubius* except for one specimen of *A. americanus*.

Greenland *Ammodytes* Since doubts exist with regard to the number of species and the appropriate names of species occurring in Greenland, these specimens were analyzed separately using the PCA equation and diagnoses used in analyzing and describing the species in other regions. Only those specimens (N = 51) with complete meristic data were included in the analysis. The majority of specimens fit our definition of *A. dubius*. Vertebral counts ranged from 66 to 75 ($\bar{x}$ 70.8); plicae counts from 124 to 156 ($\bar{x}$ 133.4); PCA scores from 1388 to 1636. Two specimens, however, fit our definition of *A. americanus*; one specimen had 70 vertebrae, 123 plicae, and a PCA score of 1374, and the other had 68 vertebrae, 124 plicae, and a score of 1372.

Discussion

Results of this study demonstrate, in accordance with the majority of previous research (Richards et al. 1963, Leim and Scott 1966, Winters 1970, Scott 1972, Richards 1982), that two species of sand lances occur in the western North Atlantic: an inshore species, *A. americanus*, with low meristic features, and an offshore species, *A. dubius*, characterized by high meristics.

No unequivocal method has been demonstrated previously to consistently identify individuals of *A. americanus* and *A. dubius*. Counts purportedly delineating the two species varied between studies, and considerable variation in meristic features for either one or both of these species has been reported. Additionally, earlier studies relied principally on vertebral counts (with supporting data from dorsal and anal ray counts) but this approach was inadequate to accurately identify all individuals. Plicae count, the most useful character in our study, was not used in the majority of previous studies. Furthermore, the lack of published detailed locality data in the majority of previous studies, consistent inshore/offshore designations, and a full understanding of migration patterns (Reay 1970) have added to the confusion in taxonomic status and ability to accurately identify species.

With no clear-cut definition of the western North Atlantic species, identification problems have hindered previous investigators. A case in point is the reported discrepancy in geographic distribution of *A. dubius* and resultant interpretations of species. Since the earliest studies by Reinhardt (1838) and DeKay (1842), species designations have not been consistent. Reinhardt (1838) described *A. dubius* from Greenland. Jordan and Evermann (1896) later reported that this species occasionally reached as far south as Cape Cod. In the revision of the Ammodytidae by Duncker and Mohr (1939), *A. dubius* was reported from throughout the North Atlantic. However, the majority of recent researchers disagree and have limited the range of *A. dubius* to the western North Atlantic. In 1963, Richards et al. reported *A. dubius* as extending

further south to Virginia (37°N). Later Richards (1982), for no stated reason, reported a more limited distribution for *A. dubius*, with no individuals found further south than the Scotian Shelf. Winters and Dalley (1988) also reported *A. dubius* as ranging no further south than Georges Bank.

Restricting the southern limit of the range for *A. dubius* to Georges Bank creates several problems, in particular the explanation of a southern offshore, high-meristic form. Richards et al. (1963), Richards (1982), and Winters and Dalley (1988) recognized two populations of *A. americanus* in southern waters: one an inshore low-meristic form, and the other an offshore, intermediate- to high-meristic form. This conclusion seems to stem from Perlmutter's (1940) recognition of two offshore populations, one occurring north and one south of Cape Cod, which were designated as subspecies of *A. tobianus*. In those studies (Richards et al. 1963, Richards 1982, Winters and Dalley 1988), *A. americanus* was probably chosen for the species name for southern offshore specimens because meristic values (vertebrae, dorsal and anal fin rays) were more similar to the counts they found for *A. americanus* than for northern *A. dubius*. However, all of these studies reported and accepted the existence of a north-south and/or an inshore-offshore cline for at least one (but not always the same) species. Furthermore, the offshore *A. americanus* occupied the habitat commonly inhabited by *A. dubius*. Also, the morphometric description given by Winters and Dalley (1988) for their southern offshore *A. americanus* was the same as that for their *A. dubius*. Meristic differences between inshore and offshore *Ammodytes* in southern waters are consistent with a hypothesis of two distinct sympatric—but not necessarily syntopic—species, *A. americanus* and *A. dubius*, occurring in these waters. Additionally, meristic variation between northern and southern offshore forms supports the hypothesis of geographic intraspecific variation for *A. dubius*. The data are not consistent with a hypothesis recognizing only *A. americanus* in the southern region.

Misconceptions regarding species designations of western North Atlantic *Ammodytes* are further compounded by the tendency of some authors (Richards et al. 1963, Winters and Dalley 1988) to create three groups—a low, intermediate, and high meristic group—within their data sets to explain the variation, instead of recognizing geographic variation in the offshore species. Recognizing three groups results in considerable overlap between groups, thus adding to the difficulty of identifying species. Modal analysis (only for vertebrae; Winters and Dalley 1988) in some cases seems to identify modes that are not immediately obvious in the accompanying figures or data. The accuracy of identifying groups within collections, let alone individuals, is questionable using this method. The number of components and first estimates of the modes and standard deviation must be specified first. Additionally, as Winters and Dalley (1988) point out, the reported high standard error for certain modes indicates that these means are estimated poorly.

To eliminate confusion or guesswork surrounding identification of individuals of *Ammodytes*, it was necessary to devise an objective method of identification. PCA achieves this goal since this method identifies patterns of variation between individuals without regard to the groups represented. PCA scores were utilized as a tool to summarize the data and to verify the usefulness of these meristic characters. A plot of the component scores of 332 individuals clearly showed two groups (Fig. 4). Further testing showed that these groups represent the two species. Thus, the two species can be separated using meristic characters instead of morphometric ratios of questionable validity (i.e., length-weight; see Scott 1972) with little overlap.

Furthermore, by designating a component score boundary between the two groups, the two species are clearly defined and meristic variation can be delimited for each of the two species. This is particularly important for individuals with intermediate counts, especially those occurring in collections containing both species. These individuals were the hardest to identify, but defined limits for plicae, vertebral, and dorsal ray counts made identifications easier.

To support our data analysis, a comparison with Perlmutter's 1940 data was made (Table 7; in the present study, Northern = Labrador and Quebec–Nova Scotia, Southern = Maine–Massachusetts and New York–North Carolina). The Perlmutter (1940) data were utilized because the data collected and geographic locations were similar. Designations of north-south as well as inshore-offshore locations were given also. Means for meristic data were surprisingly similar between the two studies.

Perlmutter (1940) recognized north-south and inshore-offshore clines in his data, yet misinterpreted these results. He designated several subspecies within a single worldwide polytypic form instead of recognizing geographic variation within two parapatric species. Evidence for recognition of two species is that both species have been collected in sympatry in coastal waters, particularly in the Newfoundland area. It has been postulated that *A. dubius* spawns inshore along the Newfoundland coast (Dalley and Winters 1987). The continued occurrence of high meristic individuals inshore suggests that these species are reproductively isolated (Winters and Dalley 1988). Our data provide additional support for recognition of two parapatric species since there tend to be ecological differences between the species, in particular, habitat preference.

Table 7
Comparison of mean meristic values for characters used by Perlmutter (1940) and in the present study.

	Perlmutter (1940) $\bar{x}$	Nizinski et al.[1] $\bar{x}$
Vertebrae[2]		
A. americanus		
Northern	67.3	67.0
Southern	65.5	65.2
A. dubius		
Northern	73.5	72.0
Southern	70.0	70.2
Dorsal rays		
A. americanus		
Northern	57.0	57.3
Southern	55.3	56.9
A. dubius		
Northern	63.3	62.8
Southern	60.3	61.3
Anal rays		
A. americanus		
Northern	28.8	29.5
Southern	27.6	29.1
A. dubius		
Northern	32.3	32.1
Southern	29.6	30.6
Pectoral rays		
A. americanus		
Northern	13.2	13.1
Southern	13.7	13.3
A. dubius		
Northern	14.4	14.0
Southern	14.2	14.0

[1]Northern = Labrador and Quebec–Nova Scotia
Southern = Maine–Massachusetts and New York–North Carolina
[2]Hypural plate excluded.

The majority of individuals have been collected either inshore (*A. americanus*) or offshore (*A. dubius*) with little syntopic occurrence. We conclude, therefore, that two distinct species, *A. americanus* and *A. dubius*, occur in the western North Atlantic Ocean.

A similar case has been reported for the species of *Ammodytes* (*A. personatus* and *A. hexapterus*) found off Japan. Populations of morphologically and meristically similar individuals are difficult to distinguish from one another. Electrophoretic data, however, suggest that two sympatric, genetically distinct groups do occur among these *Ammodytes* species (Okamoto 1989). Perhaps a similar analysis is needed for the western North Atlantic ammodytids to confirm species designations.

As previously mentioned, this study is a preliminary step toward understanding a more complex problem. Many other questions, including the taxonomic status of Greenland *Ammodytes*, remain unanswered. Specimens examined in our study ($N = 51$) had high counts, similar to those obtained for *A. dubius*. But counts for these individuals were highly variable and did not agree completely with those of *A. dubius* from the western North Atlantic. In particular, some specimens had low vertebral counts and extremely high plicae counts. Others with low plicae counts, albeit still in the range for *A. dubius*, tended to have high vertebral counts. Based on meristic combinations and computed PCA scores, the Greenland sand lance is most similar to *A. dubius*. This finding adds to the existing conflict over which species are found in Greenland. Published accounts indicate two species of sand lances occur in this region: high-meristic *A. dubius*, and a low-meristic, inshore species that has been called *A. marinus* by Winters and Dalley (1988) as were all western Atlantic *A. americanus*. However, there is some question to the identity of the low-meristic sand lance occurring in Greenland. Counts for these specimens match those of *A. americanus* as well as the European *A. marinus*. The low-meristic Greenland species has reportedly been dipnetted and seined on shallow beaches and in protected fjords. *Ammodytes marinus*, on the other hand, is described as the commonly occurring offshore, deeper-water species in the eastern North Atlantic (Richards et al. 1963, Wheeler 1969, Reay 1970), although this species has also been reported from inshore stations (Raitt 1934, Kirillov 1936).

A limited number of *A. marinus* from the British Isles were examined; however, the data from these fish posed more questions than solved existing problems. Meristic features of these specimens spanned the ranges recorded for *A. americanus/dubius*, and morphological differences between these three species were not distinctive. The problem is further complicated since *A. dubius* and *A. marinus* are believed to be on opposite shores of the Atlantic (Reay 1970) yet both have been reported from Greenland. The taxonomic status of *Ammodytes* occurring in Greenland waters cannot be resolved until meristic and geographic ranges of European *A. marinus* are determined.

Taxonomic confusion is not restricted to Atlantic species; the taxonomy of North Pacific *Ammodytes* is problematical as well. Researchers agree that *A. hexapterus* and *A. personatus* occur in Japanese waters (Kitaguchi 1979, Hashimoto 1984), with *A. hexapterus* reported as the more northern species and *A. personatus* as the more southerly species. But these species also are similar morphologically and have overlapping counts (vertebrae and dorsal and anal fin rays). Additionally, high variability with two existing modes in the meristic data suggest the presence of two subpopulations in the southern *A. personatus* group (Hashimoto

and Kawasaki 1981, Hashimoto 1984). Isozyme differences have indicated three separate genetic stocks (one *A. hexapterus* and two *A. personatus*; Hashimoto 1984), and recent electrophoretic analysis confirms the existence of a northern and southern population of *A. personatus* as well as a possible new species or subspecies (Okamota et al. 1988, Okamota 1989). Morphological differences, however, are not significant between populations and between species, and it remains to be decided if designation of subspecies within this species complex is appropriate (Hashimoto 1984).

Problems also occur in defining limits between North Pacific and western North Atlantic species of *Ammodytes*. Some investigators (Lindberg 1937, Andriashev 1954, Walters 1955, Richards et al. 1963) have suggested that *A. hexapterus* is circumpolar and extends from the Pacific into the Arctic and North Atlantic oceans. These workers have argued that *A. hexapterus* is synonymous with *A. americanus* and/or *A. marinus*. A limited number of *A. hexapterus* ($N = 5$) from Alaska and *A. marinus* ($N = 15$) from the British Isles were examined and no distinct morphological or meristic characters were found to clearly separate these species from those occurring in the western North Atlantic. Both *A. hexapterus* and *A. marinus*, however, are usually characterized as occurring in deeper, offshore waters. Obviously, the entire genus is in need of revision.

Acknowledgments

For loan or donation of material, we thank Kenneth W. Able (Rutgers University), Eugenia B. Böhlke (ANSP), Bruce Burns (NMFS Narragansett Laboratory), Barry Chernoff (FMNH), Michael P. Fahay (NMFS Sandy Hook Laboratory), William L. Fink (UMMZ), Karsten E. Hartel (MCZ), Don E. McAllister (NMC), John A. Musick (VIMS), Gareth Nelson (AMNH), Jørgen G. Nielsen (ZMUC), and Lou Van Guelpen (ARC). The NMFS Woods Hole Laboratory assisted in the collection of fresh material. A large file of radiographs of *Ammodytes*, made to search for vertebral anomalies, was loaned to us by the NMFS Oxford Laboratory. James D. Felley provided statistical advice. Frank P. Almeida, NMFS Woods Hole Laboratory, supplied the data for Figure 1. Figure 3 was drawn by Keiko Hiratsuka Moore. Douglas W. Nelson (UMMZ) provided a xerox copy of Perlmutter's unpublished dissertation. Drafts of the manuscript were reviewed by Kenneth W. Able, Laurence Buckley, Michael P. Fahay, Irv Kornfield, Thomas A. Munroe, Theodore W. Pietsch, and Sarah W. Richards. G.H. Winters critically reviewed several drafts of the manuscript and many of his comments were useful in revising the paper, although we do not agree on the interpretations of some aspects of geographic variation in *Ammodytes*.

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Appendix 1: Material examined

Abbreviations of institutions

AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
ARC	Atlantic Reference Centre, Huntsman Marine Laboratory, St. Andrews, New Brunswick
FMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
NMC	National Museum of Natural Science, Ottawa, Canada
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, MI
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC
VIMS	Virginia Institute of Marine Science, Gloucester Point, VA
ZMUC	Kobenhavns Universitet Zoologisk Museum, Copenhagen, Denmark

Material is listed by species, geographically from north to south.

Ammodytes americanus

Labrador 177 specimens (49–157 mm SL) from nine collections. FMNH 31106–31116, 31118–31132 (25, 49–126) Anatalak Bay, Nain, Labrador; July–Aug. 1928. MCZ 12471 (8, 98–143) Labrador. MCZ 12480 (52, 80–145) Labrador. MCZ 12481 (17, 105–157) Labrador; Packard; 1865. MCZ 12482 (30, 85–155) Labrador. MCZ 51802 (4, 69–76) Hamilton Inlet, Collingham's Cove; *Blue Dolphin*; 7 Feb. 1952. USNM 165262 (1, 96) Indian Cove, Assyis Run, St. Lewis Sound, 52°15′N 55°04′W; *Blue Dolphin*; 12 July 1949. USNM 165300 (35, 96–147) Labrador, Hare Harbor, 53°43′N 56°46′W; *Blue*

Dolphin; 2 July 1950. USNM 165371 (5, 92–104) Labrador, mouth of Tessiujarsuk near Nain; *Blue Dolphin*; 8 Aug. 1951.

Newfoundland, Nova Scotia, and Quebec 90 specimens (52–147 mm SL) from 11 collections. MCZ 49725 (1, 147) Newfoundland, Nolan's Beach, Sweet Bay, Bonavista Bay; R.H. Backus; 7 June 1948. NMC 73-380 (3, 121–140) Newfoundland; Bonne Bay at Norris Point Wharf; B.E. Bowen; 9 July 1973. NMC 66-174 (1, 80) North Newfoundland, Griguet Harbor at Griguet, 51°32.5′N 55°28.5′W; D.E. McAllister and W.H. Vliet; 0–1 m; 18 June 1966. NMC 59-266 (38, 96–140) Quebec, Perce on tip of Gaspe Peninsula, Gaspe Co. 48°30′N 64°15′W; D.E. and N.A. McAllister; 0–1 m; 10 June 1959. NMC 81-0888 (11, 76–101) Quebec, Fleuve St. Laurent, 49°35′N 67°25′W; J.D. Dutil and B. Legare; 24 June 1981. USNM 88849 (1, 131) Quebec, north side of Matamer River; Amory-Bowman Expedition; 1927. ARC 8600807 (12, 97–124) Tabusintac estuary (gulley); M.J. Dadswell and G. Melvin; 0–1 m; 20 July 1977. ARC 8600809 (1, 90) New Brunswick; New River Beach; M.J. Dadswell et. al.; intertidal; 16 Sept. 1977. ARC 8600803 (1, 114) New Brunswick, St. Andrews; Oct 1949. UMMZ 193387 (20, 52–63) New Brunswick, Miramichi, inside West End Bay du Vin Island; R.A. McKenzie; 22 July 1942. ARC 8600802 (1, 125) Prince Edward Island; Aug. 1953.

Maine and Massachusetts 285 specimens (60–168 mm SL) from 14 collections. FMNH 17181–17185 (5, 141–168) Boothbay Harbor, ME; July 1931. MCZ 44877 (2, 95–102) MA, Barnstable Harbor; J. Morin. MCZ 57161 (14, 60–121) Chatham, upper Cockle Cove off Mill Creek Rd.; K.E. Hartel. MCZ 12464 (15, 86–123) Yarmouth; L. Agassiz. UMMZ 140537 (15, 106–133) MA, beach near Scituate between second cliff and third cliff; C.L. and L.C. Hubbs; 0–3 ft; 17 June 1928. USNM 302255 (126+, 75–105) Nahant, East Point, Marine Science Institute; B.B. Collette, BBC 1759; 0–1 m; 7 Aug. 1981. USNM 302256 (11, 76–108) 41°18′N 70°28′W; *Gloria Michelle* Cr. 8592, Sta. 57; 12 Sept. 1985. USNM 83720 (15, 91–128) MA, Truro; W.C. Kendall; 14 Sept. 1892. USNM 36925 (20, 101–119) MA, Bass Rocks, New Gloucester; A.H. Clark; Oct. 1879. USNM 132092 (20, 73–115) ME, Wood Island; *Grampus*; surface; 13 Oct. 1915. USNM 73499 (3, 97–105) MA, "The Cut" and Pavillion Beach, Gloucester; *Grampus*; 29 July 1895. USNM 302254 (10, 79–112) Newberry Port, MA, Merrimack R. USNM 302253 (22, 73–122) Martha's Vineyard Sound, MA. Fahay collection (7, 80–130) Nauset Marsh, Cape Cod; Fahay and Able.

New York to Virginia 199 specimens (83–137 mm SL) from three collections. AMNH 36590 (72, 89–120) NY, Suffolk Co., Sunken Meadows' State Park, east of Jetty Seine; G.J. Nelson et al.; 19 May 1977. AMNH 37692 (30, 83–118) Suffolk Co., Gardener's Island, tidal outlet, Bostwick's Pond; D.E. Rosen et al.; 22 Apr. 1977. ANSP 165786 (97, 83–137) approx. 2.5 naut. mi. SE of Little Egg Inlet, along axis of lump-5252; C.B. Milstein, CBM 72–145.

Ammodytes dubius

Labrador 14 specimens (121–203 mm SL) from two collections. USNM 165263 (11, 121–187) Pack's Harbor, 53°54′N 56°59′W; *Blue Dolphin*; 24 July 1949. USNM 165264 (3, 143–203) Hare Harbor; *Blue Dolphin*; 2 July 1950.

Newfoundland, Nova Scotia, and Quebec 72 specimens (107-244 mm SL) from five collections. NMC 64-763 (16, 178–209) off Newfoundland, Grand Banks, 45°06′30″N 49°01′00″W; *A.T. Cameron*; 14 Oct. 1964. NMC 64-764 (11, 169–244) off Newfoundland, Grand Banks, 54°02′50″N 49°04′15″W; *A.T. Cameron*; 5 Oct. 1954. VIMS 1224 (30, 192–230) 44°05′05″N 60°04′30″W; *A.T. Cameron* Cr. 176, Sta. 16. UMMZ 201715 (14, 107–195) Nova Scotia, caught on Middle Bank of Atlantic Ocean, 44°35′N 60°25′W; *S.T. Venosta*; Nov. 1938. ARC 8600808 (1, 155) Grand Bank, SE shoal water; G. Somerville; 8 July 1954.

Maine and Massachusetts 264 specimens (77–253 mm SL) from 15 collections. MCZ 40699 (1, 177) N. end Stellwagen Bank; F. Buinett. MCZ 62955 (3, 77–102) Martha's Vineyard, just off south coast between Chilmark and Edgartown; *Gloria Michelle* Cr. 8592, Sta. 53–56. VIMS 2293 (2, 249–253) 42°36′N 66°17′W; *Albatross IV* Cr. 6911, Sta. 214. USNM 67636 (4, 83–98) MA, North Truro, Cape Cod; *Grampus*; 9 June 1896. USNM 163734 (1, 256) Georges Bank, 41°21′N 67°33′W; R.L. Wigley; 1950. USNM 302242 (6, 80–128) 40°59′N 69°(26–28)′W; *Delaware II* Cr. 8207, Sta. 91; 44 m; 13 Oct. 1982. USNM 302245 (3, 112–122) 40°49′N 69°04′W – 40°48′N 69°05′W; *Delaware II* Cr. 8207, Sta. 92; 69 m; 14 Oct. 1982. USNM 302247 (15, 98–123) 41°21′N 67°26′W; *Delaware II* Cr. 8207, Sta. 123; 38 m; 21 Oct. 1982. USNM 302258 (55, 87–125) 41°28′N 67°46′W; *Delaware II* Cr. 8207, Sta. 124; 40 m; 21 Oct. 1982. USNM 302250 (26, 86–142) 41°33′N 67°58′W; *Delaware II* Cr. 8207, Sta. 125; 30 m; 21 Oct. 1982. USNM 302240 (17, 96–140) 41°38′N 68°27′W; *Delaware II* Cr. 8207, Sta. 128; 60 m; 22 Oct. 1982. USNM 302249 (10, 87–128) 41°35′N 66°58′W; *Delaware II* Cr. 8207, Sta. 143; 58 m; 23 Oct. 1982. USNM 302248 (50, 121–175) 41°51′N 70°29′W; *Gloria Michelle* Cr. 8592, Sta. 3; 13 m; 6 May 1986. USNM 302246 (45, 59–184) 41°35′N 69°56′W; *Gloria Michelle* Cr. 8592, Sta. 77; 7 m; 18 May 1986. USNM 302251 (46, 100–161) 42°05′N 70°08′W; *Gloria Michelle* Cr. 8592, Sta. 91; 16 m; 18 Sept. 1985. USNM 302257 (17, 84–108) 41°18′N 70°28′W; *Gloria Michelle* Cr. 8592, Sta. 57; 12 Sept. 1985.

New York to North Carolina 415 specimens (54–249 mm SL) from 24 collections. ANSP 36662-73 (13, 146–207) NJ, Carson's Inlet, Cape May Co.; R.J. Phillips; 1 Nov. 1908. VIMS 2294 (3, 175–193) 41°2.5′N 69°00′W; *Albatross IV* Cr. 7002. VIMS 2295 (19, 194–249) 39°03′N 73°41′W; *Albatross IV* Cr. 6908, Sta. 161. VIMS 2390 (1, 217) 28°28′N 74°37′W; *Sea Breeze*, Sta. T350. VIMS 2807 (3, 98–109) 37°51′N 75°08′W; McEachran. VIMS 2808 (9, 140–178) 38°07′N, 74°44′W; *Albatross IV* Cr. 6920, Sta. 2. VIMS 7377 (1, 186) 37°01′N 74°57′W, Virginia Shelf; *Captain Wool*. VIMS 7751 (4, 120–190) 40°47′N 69°40′W; *Albatross IV* Cr. 8005, Sta. 36, ANSP 165785 (153, 92–138) approx. 2.5 naut. mi. SE of Little Egg Inlet, along axis of lump-5252; C.B. Milstein, CBM 72–145. UMMZ 212624 (50, 100–185) NY, Plum Beach, Long Island; A. Perlmutter; 20 Dec. 1937. USNM 302243 (1, 159) 40°00′N 73°47′W – 40°01′N 73°44′W; *Delaware II* Cr. 8207, Sta. 44; 29 m; 8 Oct. 1982. USNM 302244 (3, 119–143) 41°11′N 71°24′W – 41°13′N 71°24′W; *Delaware II* Cr. 8207, Sta. 75; 38 m; 11 Oct. 1982. USNM 302241 (46, 54–182) 41°40′N 69°54′W; *Gloria Michelle* Cr. 8592, Sta. 78; 12 m; 19 May 1986. USNM 302229 (1, 132) 38°52′N 74°48′W; *Albatross IV* Cr. 8809, Sta. 78; 6.6 fm; 22 Sept. 1988. USNM 302230 (1, 117) 40°50′N 72°(22–24)′W; *Albatross IV* Cr. 8809, Sta. 135; 18 m; 27 Sept. 1988. USNM 302231 (1, 117) 36°55′N 75°52′W; *Albatross IV* Cr. 8809, Sta. 60; 5.7 fm; 19 Sept. 1988. USNM 302232 (15, 144–171) 39°24′N 73°29′W – 39°25′N 73°26′W; *Albatross IV* Cr. 8809, Sta. 95; 38 m; 23 Sept. 1988. USNM 302233 (25, 117–146) 38°47′N 74°08′W – 38°49′N 74°09′W; *Albatross IV* Cr. 8809, Sta. 84; 44 m; 22 Sept. 1988. USNM 302234 (1, 132) 40°40′N 72°58′W – 40°41′N 72°56′W; *Albatross IV* Cr. 8809, Sta. 130; 15 m; 26 Sept. 1988. USNM 302235 (20, 144–171) 39°23′N 73°43′W – 39°24′N 73°42′W; *Albatross IV* Cr. 8809, Sta. 94; 32 m; 23 Sept. 1988. USNM 302236 (2, 121–122) 37°(04–06)′N 75°18′W; *Albatross IV* Cr. 8809, Sta. 56; 27 m; 18 Sept. 1988. USNM 302237 (1, 125) 39°19′N 74°(21–23)′W; *Albatross IV* Cr. 8809, Sta. 88; 10 m; 22 Sept. 1988. USNM 302238 (24, 100–138) 36°46′N 75°24′W – 36°47′N 75°22′W; *Albatross IV* Cr. 8809, Sta. 54; 23 m; 18 Sept. 1988. USNM 302239 (18, 104–189)

38°47′N 73°15′W – 38°48′N 73°13′W; *Albatross IV* Cr. 8809, Sta. 3; 80 m; 13 Sept. 1988.

Ammodytes sp.

Greenland 55 specimens (48–192 mm). USNM 87373 (5, 48–55) P.H. Sorenson. MCZ 63338 (4, 63–77) 64°47.3′N 30°37.4′W; *Endevor* Cr. 133, Sta. 5. MCZ 63339 (2, 55–59) 65°23′N 29°22.8′W; *Endevor* Cr. 133, Sta. 12. ZMUC various lots (44, 57–192): 61150; store Hellefiskebanke, 24 Hum v.s.v. f. Rifkol, smaa sten; 10 July 1912; *Beskytteren*. P61152. P61153. P61154. P61158; Godhavn; Porsild. P61159; Bunden af. Kapisigdlitfjord øf lak seelven Aalehaandvaad; *Dana*, Sta. 2325. P61166; Greenland 66°44′N 53°W; *Dana*, Sta. 2349. P61312; Prøvens Havn, NV Grønland; Finn Salomonsen. P61322. P61324. 73; Grønland. 76. 78. 79. 84; 23/2, 49; N. 101. 89; Grønland. 9Od. 67°53′N 54°02′W. 121. 160; Jakobshavn; P. Müller. 161; Jakobshavn; P. Müller. 162; Claushavn; Ad. Jensen. 163; Disko Bügten. 165; Marrak i Sydostbugten, Opskyllet i Beg. af., Aug. 1906; Ad. Jensen. 169; Tkamiut i Sydostbugten; Lohmann. 170; Godhavn; Porsild. 176; Sukkertoppen; Bistrup. 178; Sukkertoppen; Bistrup. 179; Sukkertoppen; Bistrup. 180; Sukkertoppen; Bistrup. Uncat (15 spec.); Kigdluf Iluat, Grønland, 63°53′N 51°22′W.

Ammodytes marinus

USNM 302259 (2, 115–126) Brunswick Wharf; Thames and Wheeler. USNM 302260 (8, 88–148) Littlebrook and W. Thurrock; Thames. USNM 108812 (5, 160–171) British Isles; Firth of Forth, 56°12′N 2°43′W.

A. hexapterus

USNM 207553 (1, 159) AK, Cook Inlet, N. Barren Islands, S of Kenai Peninsula, 59°09′N 152°17′W; *Yaquina*; 60 fm; 30 July 1963. USNM 235313 (2, 91–143) AK, Aleutian Islands, NE Adak Island, southside of Clam Lagoon; J. Rosewater and P.R. Greenhall; 8 June 1979. USNM 266655 (2, 123–129) AK; *Miller Freeman*, Sta. B44; 14 Aug. 1982.

Determination of Factors Affecting Recruitment of Chinook Salmon *Oncorhynchus tshawytscha* in Central California

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Abstract.– We computed correlations between various population estimates for Central California chinook salmon *Oncorhynchus tshawytscha* and both freshwater and marine environmental variables using methods that account for intraseries correlation in a more accurate and conservative way than those used previously. These indicated a negative influence of ENSO (El Niño-Southern Oscillation) conditions in the year during which most of these fish are caught or leave the ocean to spawn. Although freshwater environmental influences have been previously proposed on the basis of correlation analysis, and have been demonstrated using direct survival estimates based on marked fish, they were not detectable using correlation techniques that accurately account for intraseries correlation. There was also weak evidence for an influence of conditions associated with a negative upwelling index at the time chinook salmon enter the ocean. However, because these conditions are associated with high river flows in addition to oceanographic effects, these correlations may merely result from the influence of freshwater flows. To further describe oceanographic influences we computed the principal components of upwelling index, sea level height, and sea surface temperature. The first principle component, which reflected the effects of ENSO conditions in the equatorial Pacific during the previous winter, was significantly correlated with chinook salmon abundance in their final year, and marginally correlated with abundance during the first ocean summer. This work demonstrates new techniques for reducing spurious correlations and the practical difficulties involved in sorting out the multivariate influences on populations subject to remote forcing through oceanographic and meteorological conditions.

Manuscript accepted 23 January 1990.
Fishery Bulletin, U.S. 88:257–269.

Understanding the influences of environment on survival and abundance of chinook salmon *Oncorhynchus tshawytscha* is necessary for management of both fisheries and surface water in central California. The salmon fisheries are managed by allocating predicted preseason abundance between catch and spawning escapement, and flow rates in central California rivers are currently managed to allow adequate flows for spawning and rearing of chinook salmon. Better understanding of environmental influences on salmon populations could improve the ability to forecast preseason abundance and more clearly define the impacts of water management on salmon abundance.

Chinook salmon spawn in freshwater, but spend most of their lives in the ocean. In California's Central Valley, there are four distinct runs of chinook salmon named for the timing of their spawning migrations: fall, late-fall, winter, and spring. Typically over 90% of the spawning salmon are from the fall run, and over 80% spawn in the Sacramento River and its tributaries (USFWS 1987). Fall run chinook salmon migrate upstream July through November, and spawn October through January. Eggs incubate in the gravel October through March, and young fish rear in the streams and migrate downstream December through June (USFWS 1987). Most fish spawn at age 3, with some spawning at ages 2 and 4, and a few fish at age 5 (Dettman et al. 1986, Reisenbichler 1986, Kope 1987). The precocious 2-year-old spawners are primarily males and are called "jacks." While in the ocean, Central Valley chinook salmon are harvested by commercial and recreational troll fisheries. Catches in both fisheries are dominated by 3-year-old fish (Denega 1973, Kope 1987).

In addition to natural production, several hatcheries and spawning facilities produce fish to enhance the fisheries and mitigate for losses of spawning and rearing habitat resulting from water development projects (Fig. 1). The contribution of hatchery production to spawning runs has increased in recent years, and has been estimated to be approximately 15% of the total run in the upper Sacramento River (Reisenbichler 1986), 78% of the run in the Feather River, and 87% of the total in the American River (Dettman and Kelley 1986).

Numerous studies have examined relationships between environmental

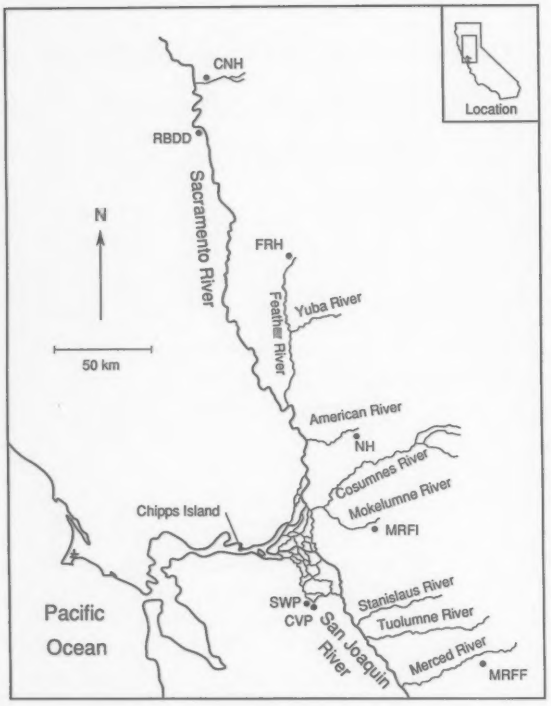

Figure 1

Chinook salmon spawning streams and fish facilities of California's Central Valley. CNH = Coleman National Hatchery; RBDD = Red Bluff Diversion Dam; FRH = Feather River Hatchery; NH = Nimbus Hatchery; MRFI = Mokelumne River Fish Installation; MRFF = Merced River Fish Facility; SWP = State Water Project pumping plant; CVP = Central Valley Project pumping plant.

variables and recruitment or abundance of Pacific salmonids through correlation analysis. Many of these studies have focused on chinook salmon (e.g., Van Hyning 1973, Barton 1980), and a few have dealt with the stock of chinook salmon that spawns in California's Central Valley. Most of these studies have detected environmental influences on recruitment; but in the case of Central Valley chinook salmon, reasonably long time-series of recruitment data have been lacking. Some analysts have therefore used estimates of spawning escapement as a proxy for past recruitment (Dettman et al. 1986, Dettman and Kelley 1986, Reisenbichler 1986, USFWS 1987). In general, these studies have reported positive correlations with flow variables and negative correlations with temperature during the period when the spawners were migrating downstream as smolts. Because of a negative correlation between flow variables and temperatures (Dettman et al. 1986), it is impossible to distinguish between effects of temperature and effects of flow using existing data. Stevens and Miller (1983) used two time-series of smolt estimates based on smolt catches in the delta (Fig. 1), and showed a positive correlation with flows in the previous winter. The most convincing studies used estimates of mortality based on the difference in survival between tagged fish released above the delta and tagged fish released below the delta to show a positive influence of flow rates in the delta and negative influences of temperature and diversions (Kjelson and Brandes 1989, Kjelson et al. 1981, USFWS 1987, Dettman et al. 1986).

In contrast to those of freshwater, potential marine influences on Central Valley chinook stocks have not been explored. Oceanographic conditions off the California coast vary dramatically providing potentially important interannual differences in predators, prey, transport, and ocean temperature during the marine phase of chinook salmon life. The normal pattern of circulation in the northeastern Pacific involves northwesterly winds of varying strength along the coast of California in the spring and summer months which reinforce the geostrophic flow of the California Current and transport surface waters offshore (Mysak 1986, Hickey 1989). This causes varying degrees of upwelling of deeper water and longshore advection of subarctic water along the coast of California and Oregon, which are associated with colder temperatures and depressed sea level heights. The amount of upwelling is estimated by an upwelling index based on winds computed from measured atmospheric pressure gradients (Bakun 1975). Occasional El Niño-Southern Oscillation (ENSO) events, characterized by a warming of equatorial Pacific waters, have a dramatic effect on California coastal waters. These effects may result from either coastal trapped waves which propagate poleward from the Equator, or an atmospheric teleconnection between the Equator and midlatitudes (Emery and Hamilton 1985, Mysak 1986). The former would cause higher sea surface temperatures and sea level heights, but would not necessarily affect Bakun's upwelling index (Enfield and Allen 1980, Emery and Hamilton 1985, Mysak 1986). The latter involves an increase in strength of the Aleutian low-pressure system and a weakening of the north Pacific high-pressure system. Changes in the atmospheric pressure gradients, associated with ENSO events, weaken the northerly winds which results in less upwelling, warmer sea temperatures, higher sea level, and a lower upwelling index (Norton 1987, Mysak 1986). ENSO events and anomalous strengthening of the Aleutian low pressure system may occur at the same time, but each also occurs alone (Emery and Hamilton 1985, Mysak 1986).

Marine and freshwater influences on California Central Valley chinook salmon could be confounded. Large-scale oceanographic and meteorological conditions in

the Pacific have been related to precipitation in California, which could in turn influence flow rates. Markham and McLain (1977) found a positive correlation between California rainfall and sea surface temperature off the coast of Washington. However, rainfall in California is only weakly related statistically to equatorial conditions associated with ENSO events (Douglas and Englehart 1981, Cayan and Peterson 1989, Redmond 1988).

Environmental influences on fish populations are often explored by computing correlations between environmental and population time-series; however, these are computed and the significance of resulting correlations are evaluated in a variety of ways. In attempting to detect environmental influences by computing correlations, the probability of obtaining a significant result is often artificially inflated by two problems: (1) intraseries correlation and (2) multiple tests (cf. Walters and Collie 1988). The latter arises from the fact that many environmental series can be tested for correlation with the population series; hence the probability of falsely identifying a significant relationship is greater than the probability level of each test. Methods exist for dealing with both problems, but we focus on the former here [see Hollowed et al. (1987) and Drinkwater and Myers (1987), for examples of dealing with the latter]. The former, intraseries correlation, is a lack of statistical independence of observations, which implies that the true number of degrees of freedom that should be used in determining the significance of a computed correlation is less than the number of points in the series. There are two steps that can be taken to deal with this problem: (1) removing as much of the intraseries correlation as possible, and (2) accounting for the remaining correlation in the computation of confidence limits.

Removal of intraseries correlation can be accomplished by arbitrarily "pre-whitening" the series (i.e., filtering the series so that correlation between adjacent points is removed) (Box and Jenkins 1976, Fogarty 1988), but is more directly justified when there is a physical basis for doing so and the new series represents a meaningful quantity. In the case of an abundance or catch series, one can compute a recruitment time-series from the original series using deconvolution (Kope and Botsford 1988). Deconvolution is a procedure based on the observation that catch or abundance is a sum over age-classes which is essentially a weighted sum over past recruitment (i.e., a moving average), in which the weighting factors are the (assumed constant) probabilities of survival to each age. If the abundance or catch series is established using a size limit, rather than an age limit, the numbers at each age that are larger than the size limit must also be accounted for in the weighting factors. Deconvolution inverts this summing process to give recruitment in terms of catches or abundances. Deconvolution provides two advantages over using the catch or abundance series without deconvolution: (1) it removes the intraseries correlation due to summing ages in abundance or catch data, and hence provides more conservative estimates of the significance of correlations between recruitment and the environment; and (2) it yields an estimate of recruitment from the abundance or catch data, hence it can also increase the magnitude of estimated correlation coefficients. However, deconvolution cannot yield an exact value of recruitment when noise is present in the abundance or catch data. The error present in the recruitment estimates depends on the error present in the catch or abundance series and on the stability of the deconvolution (Kope and Botsford 1988). Thus, there is a trade-off between the two advantages of removing the effects of multiple age-classes and the disadvantage of amplifying errors that depends on the stability of the deconvolution and the magnitude of measurement errors in abundance. Consequently, deconvolution may not always be useful.

Intraseries correlation is accounted for in the computation of confidence limits by estimating the variance of the computed correlation coefficient in a way that accounts for the intraseries correlation. This often involves using one of the many approximations to an expression originally due to Bartlett (1946) (Box and Jenkins 1976, Chelton 1984, Botsford 1986). This approach is functionally equivalent to adjusting the number of degrees of freedom using a variation of the expression originally due to Bayley and Hammersley (1946) (Sutcliffe et al. 1976, Drinkwater and Myers 1987). We use another method for dealing with this problem that leads to an actual probability of detection that is closer to the specified probability than other methods (Kope and Botsford 1988, Botsford and Wainwright unpubl.).

In spite of the fact that greater intraseries correlation artificially inflates the probability of detecting a significant relationship, some researchers have added intraseries correlation to the time-series before computing correlations. For example, in the freshwater chinook salmon studies cited above, Dettman et al. (1986) and Reisenbichler (1986) used 2-year moving averages of both spawning escapement and environmental variables in an effort to reduce the effects of age structure in the spawning escapement data. Hollowed et al. (1987) used five-point moving averages in their analysis of recruitment patterns in the northeast Pacific. Because the effects of intraseries correlation were not accounted for in either of these studies, the use of moving averages would decrease the probability of detecting real correlations and increase the probability of spurious correlation (Kope and Botsford 1988). Others have used moving averages before computing

correlations, but then have attempted to account for increased intraseries correlation [cf. Drinkwater and Myers (1987), who use a modified form of the Bayley and Hammersley (1946) approach].

The goals of the study reported here are to explore potential environmental influences on chinook salmon populations in California's Central Valley, and to demonstrate the effective use of some recently developed methods of correlation analysis that are more realistic and conservative than those used previously. We identify potential oceanographic environmental influences on these populations and show that the freshwater influences, which were established by direct survival estimates (USFWS 1987, Kjelson and Brandes 1989), are not detectable from correlation analysis of the available environmental and population data.

Data and methods

Environmental data were obtained from four sources. Average monthly streamflow data were obtained from published USGS records for gauging stations at Verona on the upper Sacramento River, Nicholas on the Feather River, and Fair Oaks on the American River. Flow and diversion data for the Sacramento-San Joaquin delta were obtained from the California Department of Water Resources DAYFLOW hydrological model. Data on sea surface temperature at the Farallon Islands, southern oscillation index, and tidal height at San Francisco (37.48 N 122.22 W) were obtained from D. Cayan (Scripps Inst. Oceanography, La Jolla, CA 92037), and calculated coastal upwelling index at lat. 39°N (Bakun 1975) was obtained from A. Bakun (Pacific Fish. Environ. Group, Natl. Mar. Fish. Serv., NOAA, Monterey, CA 93940).

Population data were taken from the recreational fishery, the commercial fishery, and spawner estimates. We used spawner data from the upper Sacramento River, the Feather River, the Yuba River, and the American River. In the available data, adults had been separated from jacks on the basis of length. Fish less than 60.7 cm fork length were taken to be jacks and larger fish were counted as adults. For the period 1970–86, spawning stock estimates were obtained from Pacific Fishery Management Council (PFMC) reports. For the years 1962–69, total fall-run spawners were taken from Fry and Petrovich (1970), and adult spawners were estimated by multiplying the total estimate of fall-run spawners in each stream by the fraction of carcasses classified as adults in the spawning stock surveys. In addition to abundance indices from individual streams, total adult spawners for the entire Central Valley were estimated by multiplying the fraction of adults reported in all spawning stock surveys each year by the number of spawners in all runs for all rivers combined.

Commercial and sport catch south of Point Arena were obtained from PFMC reports for the years 1971–86, and from L.B. Boydstun (Calif. Dep. Fish Game, Region II, Rancho Cordova, CA 95670, unpubl. data) for the years 1962–70. Commercial effort, measured in thousands of landings, and sport effort, measured in thousands of angler days, were obtained or calculated from the same sources. Fishing effort was used to calculate catch-per-unit-effort (CPUE) in an attempt to remove some of the effects of variable fishing effort from the catch data.

Recruitment of year-classes at the beginning of the commercial fishing season in their second year of life was estimated by deconvolution of the abundance indices using the procedure described in Kope and Botsford (1988). This involved calculating the contribution of recruitment in each year to the abundance indices in subsequent years using an age-structured catch and escapement model with population parameters estimated by separable virtual population analysis of marked hatchery fish (Kope 1987). In addition to the recruitment estimates obtained by deconvolution of the individual abundance series, we estimated recruitment by deconvolving the combined abundance series. This combined deconvolution was obtained by adding together commercial catch, sport catch, and total spawning escapement for each year, and deconvolving the combined abundance series (Kope and Botsford 1988).

Examination of the different recruitment estimates revealed that the deconvolved spawner series contained a great deal of high-frequency noise which resulted from the marginal stability of the deconvolutions of spawner indices. Because of differences in the relative contribution of each age-class, the deconvolution of total spawners was inherently much less stable than the deconvolution of adult spawners (Kope and Botsford 1988). Because recruitment estimates from spawners (adults and jacks) and adult spawners were highly correlated with one another (hence probably represent the same signal, and the deconvolved adult spawners contain less introduced error), only deconvolved adult spawners were used as recruitment estimates derived from spawning escapement.

No attempt was made to separate natural production from hatchery fish in the spawning escapement. Because of the large contribution of hatchery fish to the spawning runs (cf., Reisenbichler 1986, Dettman and Kelley 1986) and the straying of hatchery fish (Hallock and Reisenbichler 1979, Sholes and Hallock 1979), accurate estimation of the natural component of the runs was not possible.

Before computing correlations with environmental data, we tested for an influence of density on the pop-

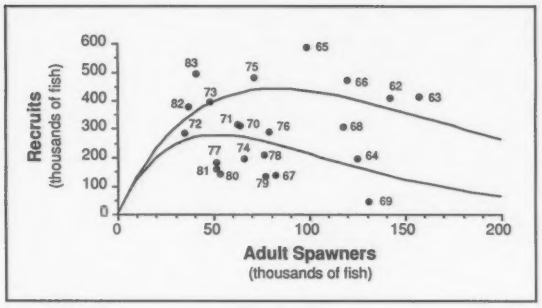

Figure 2

Chinook salmon stock-recruitment curves for the main stem of the Sacramento River. Upper curve was fitted to the data for brood years 1962–66 and the lower curve was fitted to 1967–83.

ulation series. Stock-recruitment relationships for the Sacramento, Feather, and American Rivers were examined by plotting recruitment against spawning stock, and fitting Ricker stock-recruitment curves to the data by the standard linear-regression method. This approach can result in substantial biases in the estimates of stock-recruitment parameters that result from the correlation between recruitment and subsequent spawning stock (Walters 1985, Kope 1988). However, because we use stock-recruitment curves only as a visual aid in interpreting the stock-recruitment data, potential bias was not evaluated.

To examine possible relationships between recruitment and the environment, correlations were computed between time-series of recruitment and quarterly averages of the environmental variables at all lags that had potential biological meaning. These quarterly averages are referred to as: winter, January–March; spring, April–June; summer, July–September; fall, October–December. Correlations with individual stream flows were computed at lags that corresponded to the winter, and to spring while the fish were resident in the streams as fry or migrating downstream. Correlations with delta flows and diversions were computed for the spring while the fish were migrating to sea, and correlations with oceanographic variables were computed from the spring in the year that fish migrated to sea through the summer 2 years later when most fish mature and leave the ocean to spawn. Correlations involving abundance indices (i.e., catch and spawning escapement series) were computed at lags that assumed the indices consisted primarily of 3-year-old fish.

Variability on all time scales can contribute to the variance of time-series and to the magnitude of calculated correlation coefficients. However, variability on greater than annual time scales involves intraseries correlation, which implies the effective number of degrees of freedom is less than the number of years in the series. Linear trends in the time-series reflect variability on time scales that: (a) can easily be removed by detrending, and (b) are not detectable with existing data. We have removed linear trends from our time-series because they may obscure a relationship on faster time scales.

Intraseries correlation due to variability on intermediate time scales was accounted for in evaluating the significance of computed correlation coefficients. The variance of computed crosscorrelation coefficients can be approximated by

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \sum_{i=1-n}^{n-1} \left(1 - \frac{|i|}{n}\right) \rho_{xx}(i)\, \rho_{yy}(i) \qquad (1)$$

where n is the number of data pairs, $\rho_{xx}(i)$ and $\rho_{yy}(i)$ are the autocorrelation functions of the two time-series variables at lag i, and $r_{xy}(t)$ is the computed cross-correlation coefficient between the two time-series at lag t (Botsford and Wainwright unpubl., Kope and Botsford 1988). When no intraseries correlation is present, this expression simplifies to

$$\mathrm{Var}\,[r_{xy}(t)] \approx \frac{1}{n} \qquad (2)$$

Because the real values of the autocorrelation functions of time-series variables are unknown, and computed autocorrelation coefficients must be used instead, expression (1) can sometimes produce variance estimates smaller than expression (2). However, expression (2) places a lower bound on the possible variance of computed crosscorrelation coefficients because it approximates the variance in the best possible case, when no intraseries correlation is present. We estimated the significance of computed crosscorrelation coefficients by assuming a normal distribution with variance given by the greater of expressions (1) and (2). This strategy has performed the best in giving appropriate rejection rates in Monte Carlo simulations for independent random series with varying degrees of intraseries correlation (Botsford and Wainwright, unpubl. data).

Results

Exploration of possible density-dependence revealed no clear relationships that could be removed prior to examining the influence of environmental variables. The stock-recruitment relationship for the upper Sacramento River appears to show a decrease in the equilibrium stock size that coincides with the closure of Red Bluff Diversion Dam in 1966 (Fig. 2). This supports the

Table 1

Correlations of chinook salmon population estimates with freshwater flow variables in the Sacramento Valley, California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Feather River adult spawners	Delta diversions	1st spring	0.456**
Feather River recruits (deconvolved adult spawners)	Delta diversions	1st spring	0.424**
Total adult spawners	Delta inflow	1st spring	0.402*
	Delta outflow	1st spring	0.393*

*$p<0.10$, **$p<0.05$

Table 2

Correlations with combined California Central Valley fall-run chinook salmon spawning stock indices. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Total adults	UPW	1st spring	−0.542***
		1st summer	−0.444*
	SST	3rd spring	−0.427**
		3rd summer	−0.593***
Recruits (deconvolved adults)	SLH	3rd summer	−0.425**
	SST	3rd summer	−0.541***

*$p<0.10$, **$p<0.05$, ***$p<0.01$

argument that the decrease in recruitment is a direct consequence of the dam rather than the result of gradual habitat degradation or increasing fishing pressure (Hallock et al. 1982, Hallock 1983). A similar effect had been observed by Reisenbichler (1986) but he found that the spawning runs resulting from the 1964, 1965, and 1966 brood years were intermediate between the stock-recruit curves associated with the time periods before and after these years. With our deconvolved recruitment estimates, the 1964 brood year appears to have been abnormally low, but 1965 and 1966 appear comparable with earlier years. Data for the Feather River and the American River do not fit stock-recruitment curves as well as the Sacramento River data. Our data include few years before the damming of the Feather River and none for the American River before the construction of Nimbus Dam. On both of these rivers, the hatchery contribution to the spawning escapement is large, hence lack of a clear stock-recruitment relationship is not surprising.

To assess the influence of the freshwater environment on Sacramento Valley stocks, we computed correlations between population variables and environmental variables on three rivers—the Sacramento, the Feather, and the American—as well as the total of these three, and relevant environmental variables. Population variables were total spawners, adult spawners, jacks, and recruitment estimated by deconvolution of adult spawners. We thus tested for environmental effects on all spawners, as well as differential effects on jacks and adults, and recruitment to the adult spawner population. Environmental variables were the flow of each river, total diversions of flow in the Sacramento-San Joaquin Delta, diversions as a percentage of flow, delta inflow, and delta outflow. We present all correlations that were significant at the 0.1 level using the standard uncorrelated series test, and annotate with asterisks the significance of each of these according to the more conservative test that allows for intraseries correlation.

The results (Table 1) provide no evidence for an influence of the freshwater environment on numbers of total spawners, jacks, adults, or adult recruits to these stocks. In fact, the number of correlations significant

Table 3

Correlations between chinook salmon recruitment estimates from ocean abundance indices and environmental variables in Central California. All correlations significant at the 0.1 level using the uncorrelated series test are shown. Asterisks refer to levels of significance using the test that accounts for intraseries correlation [equation (1)].

Index	Variable	Age of influence	Correlation
Commercial catch	UPW	1st fall	0.397*
	SLH	1st fall	−0.415**
	SST	2nd spring	−0.437*
		3rd summer	−0.503**
Recreational catch	SST	1st spring	0.711*
		1st summer	0.484**
		2nd winter	0.578
Commercial CPUE	UPW	1st spring	−0.607
		1st summer	−0.448
Recreational CPUE	SST	1st spring	0.583
		2nd winter	0.500
	UPW	1st spring	−0.453
		2nd winter	−0.357
Recruits (deconvolved commercial catch)	UPW	1st spring	−0.460**
	SST	3rd spring	−0.335
Recruits (deconvolved recreational catch)	SST	1st spring	0.353*
Recruits (combined deconvolution)	UPW	1st spring	−0.476**
	SST	3rd summer	−0.538**

*$p<0.10$, **$p<0.05$

at the 0.1 level is half the number expected if all series were independent (i.e., 4 versus 8 out of 80), and the only correlations significant at the 0.05 level using the conservative test—a positive effect of diversions on Feather River fish—has no apparent physical or biological explanation, because diversions during downstream migration would be expected to have a negative effect on survival. We consider this one a spurious correlation. Lack of correlation with delta diversions and total delta outflow may be due in part to the fact that hatcheries on the Feather and American Rivers have released most of their smolts below the delta since the mid-1970s.

Marine influences on spawners were assessed by computing correlations between the same population variables and upwelling index, sea level height, and sea surface temperature. The resulting correlations (Table 2) are significant at the 0.05 level only for adult spawners and recruitment to the adult spawner population. They show a negative influence of conditions associated with ENSO events (i.e., higher ocean temperatures, higher sea levels) in the third spring and summer, immediately before the adults enter the rivers to spawn. There is also a positive correlation with upwelling index in the first spring and summer, during which smolts migrate downriver, through the delta, and enter the ocean.

We also tested for marine and freshwater influences on catch data from both the commercial and the recreational fishery. We attempted to remove the effects of fluctuations in effort from the catch by computing commercial catch-per-unit-effort and recreational catch-per-unit-effort using the marginal effort data. We computed recruitment estimates from deconvolution of each of these. There is a substantial number of correlations significant at the 0.1 level using the standard test, but none reflect freshwater influences (Table 3). Of the correlations that are significant at the 0.05 level, two are with temperature in the third summer, and the remaining four are in the first marine year, three of them being with upwelling index and the other with sea level height. None of the catch-per-unit-effort variables were significantly correlated with any of the environmental variables using the conservative test.

These results indicate that oceanographic conditions during the first and third years of life may influence

Table 4

Autocorrelations of the Southern Oscillation Index (SOI) and crosscorrelations between SOI and oceanographic variables off Central California. UPW = upwelling index, SLH = sea level height, SST = sea surface temperature, PC = principal component. Underlined correlations correspond to an influence of previous SOI on winter oceanographic conditions off California.

	SOI	UPW	SLH	SST	1st PC
Winter SOI					
−9 mo	0.552***	0.478***	−0.205	0.000	−0.253
−6 mo	0.730***	0.261	−0.211	−0.093	−0.279
−3 mo	0.811***	0.208	−0.439**	−0.405**	−0.390*
0	1.000***	0.667***	−0.651***	−0.573***	−0.712***
3 mo	0.256	0.380*	−0.342*	−0.305	−0.449**
6 mo	0.031	−0.140	−0.270	−0.108	−0.168
9 mo	−0.110	0.231	−0.239	−0.133	10.163
12 mo	−0.131	−0.034	−0.042	−0.103	−0.078
Spring SOI					
−9 mo	0.112	0.340*	−0.102	−0.088	−0.202
−6 mo	0.115	0.113	−0.117	−0.330	−0.321
−3 mo	0.256	−0.050	−0.169	−0.165	−0.030
0	1.000***	0.393*	−0.268	−0.298	−0.414*
3 mo	0.825***	0.022	−0.297	−0.328	−0.326
6 mo	0.688***	0.246	−0.540***	−0.402**	−0.406*
9 mo	0.562***	0.424**	−0.389	−0.518***	−0.531***
12 mo	−0.224	−0.094	−0.067	−0.212	−0.129
Summer SOI					
−9 mo	−0.154	0.143	0.190	0.029	−0.070
−6 mo	0.031	−0.091	−0.037	0.007	0.092
−3 mo	0.825***	0.390*	−0.242	−0.191	−0.353
0	1.000***	0.269	−0.337*	−0.350*	−0.448**
3 mo	0.785***	0.200	−0.573***	−0.572***	−0.507***
6 mo	0.761***	0.428**	−0.433**	−0.535***	−0.544***
9 mo	0.109	0.197	−0.147	−0.337	−0.301
12 mo	−0.214	−0.256	−0.021	0.047	0.090
Fall SOI					
−9 mo	−0.110	−0.175	0.063	0.128	0.197
−6 mo	0.688***	0.426**	−0.324	−0.246	−0.406*
−3 mo	0.785***	0.305	−0.211	−0.192	−0.309
0	1.000***	0.164	−0.441**	−0.344*	−0.346
3 mo	0.835***	0.504***	−0.630***	−0.479***	−0.604***
6 mo	0.114	0.233	−0.341*	−0.314	−0.385*
9 mo	−0.152	−0.269	−0.123	0.043	0.010
12 mo	−0.072	0.263	−0.044	0.087	−0.031

*$p<0.10$; **$p<0.05$; ***$p<0.01$

these stocks of chinook salmon. However, because the correlations are with three oceanographic variables rather than consistently with one, they are somewhat difficult to interpret in terms of a causal mechanism. To attempt to solve this problem, we sought a single indicator of variability in the coastal ocean. We computed the principal components (Harris 1975) of variability in sea surface temperature, sea level height, and upwelling index, in the hope that they would have a meaningful physical interpretation. The resulting first principal component is larger than the second and third by about a factor of two, depending on season, and its loading is approximately equal for all three variables (positive for sea level height and ocean temperature and negative for upwelling index). Positive values of sea level height and surface temperature are consistent with the higher latitude effects of ENSO events as would be propagated by coastal trapped waves, but the negative value of upwelling index would require atmospheric teleconnection (recall the upwelling index is not a measure of actual upwelling, but an estimate based on atmospheric pressure

Table 5

Correlations between first principle component of the oceanographic variables and estimated total age-3 abundance (recreational catch + commercial catch + adult spawners) of chinook salmon in Central California.

	Season	First year	Second year	Third year
Total abundance	Winter	0.289	0.101	−0.151
	Spring	0.356*	−0.317	−0.354
	Summer	0.274	−0.139	−0.482**
	Fall	−0.115	0.114	0.080
Deconvolved total abundance	Winter	0.121	0.239	−0.139
	Spring	0.361*	−0.202	−0.319
	Summer	0.166	0.017	−0.480**
	Fall	−0.177	0.108	0.097

*$p<0.10$; **$p<0.05$

differences, cf. Emery and Hamilton 1985, Mysak 1986).

To test whether the first principle component was actually related to ENSO events, we computed lagged correlations between it and the Southern Oscillation Index (SOI), a primary indicator of ENSO events (Table 4). The results show that the first principal component is highly correlated with the Southern Oscillation Index during the previous winter. Also, in all but one instance (sea level height and spring SOI) the three oceanographic variables are correlated with SOI in the previous winter in the way that would be expected from their loading in the first principle component.

To further simplify interpretation, we attempted to use a single indicator of abundance. In correlations computed thus far, no single population variable had a demonstrably stronger relationship to environmental variables tested. We therefore used the sum of commercial catch, recreational catch, and spawner estimates as a single indicator of annual population abundance. For the corresponding deconvolved estimate we use the deconvolution of this combination of these three series, the deconvolution that was previously shown to provide the best estimate of recruitment (Kope and Botsford 1988).

The results using the first principle component and the total abundance estimate (Table 5) indicate an influence of ENSO-related conditions during the summer of the third year ($\alpha \leq 0.05$) and provide weak evidence for an influence of ENSO-related conditions during the first spring ($\alpha \leq 0.10$). These relationships are reflected in both the total abundance and the estimate of recruitment to total abundance obtained through deconvolution. The estimate of total abundance is also correlated with previously identified oceanographic variables. The correlations with spring upwelling are -0.478 ($\alpha \leq 0.10$) and -0.511 ($\alpha \leq 0.01$) for total abundance and deconvolved total abundance, respectively. The correlations with summer ocean temperature are -0.551 ($\alpha \leq 0.10$) and -0.540 ($\alpha \leq 0.05$) for total abundance and deconvolved total abundance respectively.

Discussion

The negative correlation between abundance in the third year and the first principle component of the oceanographic variables is consistent with observed effects of ENSO events on coastal oceanographic conditions and fish populations. Productivity in the California Current, as represented by zooplankton biomass, has long been known to be inversely correlated with sea surface temperature (Reid et al. 1958, Reid 1962). High productivity has traditionally been attributed to upwelling, but this explanation was recently questioned by Chelton et al. (1982) who proposed that higher zooplankton biomass resulted from increased equatorward flow in the California Current. The two proposed mechanisms are difficult to separate because conditions conducive to upwelling would also increase the strength of the California Current. However, whether colder water comes from the subarctic or from deeper coastal waters, it is higher in nutrients than the warmer surface waters, hence colder ocean temperatures in the winter and spring are associated with higher productivity in the California current (Chelton et al. 1982). Effects on productivity would be most noticeable during strong ENSO events. For example, total catch and average weight of chinook salmon landed in the commercial and sport fisheries were lower during the recent 1983 ENSO event (PFMC 1984, Pearcy et al. 1985, Johnson 1988).

The weak correlation between marine environmental variables during the first summer and indices of

abundance and recruitment is of the opposite sign to that expected on the basis of these relationships between the environment and productivity. However, it is possible that because juvenile fish feed on different prey than adult fish, shifts in prey distributions in warm-water years may result in higher growth and survival rates for juveniles. Northward shifts in the distribution of larval clupeids have been documented in warm-water years (Radovich 1959, 1961), and larval anchovies were found closer to shore than usual during the 1983 ENSO (Brodeur et al. 1985). Larval clupeids are a principal prey of juvenile chinook salmon (Peterson et al. 1982, Pearcy et al. 1985). Data taken off the Oregon coast show no significant difference in feeding by first-year chinook salmon between 1983, a warm-water year, and the other years 1980–85 (Brodeur and Pearcy In press).

The results obtained here for freshwater influences during the downstream migration in the first year have greater implications for the general methodology of correlation analysis in fisheries than for the dependence of salmon survival on environment. Other direct observations—the fact that differences in survival between marked fish released above the delta and marked fish released below the delta is correlated with flow over 10 years (USFWS 1987)—provide convincing evidence for a negative effect of low flows in the delta. Our results merely underscore the potential for falsely identifying a suspected relationship using standard methods for computing correlations. A dependence of abundance on freshwater variables was not detected when intraseries correlation was removed, rather than artificially added, and when it was taken into account in computing correlation coefficients. Fortunately, for this case there have been direct measurements of survival, and we need not rely solely on correlation analysis of abundance and environmental data.

Although a freshwater effect is not detectable in correlations with these freshwater variables, it may provide a partial explanation for the weak correlation seen between population variables and oceanographic conditions during the first year. During the spring, the first principle component of oceanographic variables is highly correlated with total delta inflow—flow in the Sacramento, Feather, and American Rivers (0.687, 0.577, 0.610, and 0.631, all significant at the 0.01 level using the conservative test). Thus the correlation between the first principle component of oceanographic variables during the first spring may be due to occurrences in freshwater, rather than oceanographic influences.

The various relationships implied in the results of this study provide a view of remote forcing of the North American marine and terrestrial environment that may be of general utility in examining the effects of environmental variability on other species. Events in the equatorial Pacific appear to drive the oceanographic and meteorological environment in the eastern North Pacific and western North America. Autocorrelations in the SOI (Table 4) indicate that the Equatorial events are spring to winter events (i.e., in column 1, seasons within any spring-to-winter period are correlated with each other, but none are correlated with seasons in any other spring-to-winter period). The rest of Table 4 indicates that these events influence conditions in our coastal ocean only in the following winter. This "winter only" aspect of this correlation is consistent with results relating an index of atmospheric pressure conditions on the west coast of North America, the Pacific North American index to events in the equatorial Pacific (Horel and Wallace 1981). Mysak (1986) attributed this "winter only" aspect of the equatorial/midlatitude teleconnection to the requirement for strong westerlies between the equator and midlatitudes in order to advect the atmospheric Rossby waves responsible for the teleconnection to the northeast. These westerlies exist only during the winter. The covariability among our three oceanographic variables (i.e., the fact that UPW is as important as SLH and SST in the loading on the first principle component) suggests an atmospheric teleconnection with equatorial ENSO rather than a wave propagating poleward from the Equator (cf. Emery and Hamilton 1985, Mysak 1986). These variables are also related to winter rainfall in central California. For example, annual rainfall in Sacramento is significantly correlated with the first principle component and the upwelling index in winter. Flows through the Sacramento-San Joaquin Delta the following spring are in turn correlated with that rainfall, as well as winter oceanographic conditions. This remote forcing on a global scale and the associated covariability of marine and terrestrial variables further confound the identification of causal mechanisms from these kinds of data.

However, even direct measures of survival versus environmental variables do not necessarily identify mechanisms unequivocally. Covariation between flow rates, diversions, and reversed flows in the lower San Joaquin River continue to obscure the true cause of lower run size in the San Joaquin River system (Kjelson and Brandes 1989, USFWS 1987).

The differences in results between standard methods and the new methods used here are a rough measure of how much more conservative they are. At the 0.10 level, for example, the more conservative method of computing the variance of the estimate of correlation coefficient yielded significant correlations roughly half as often as standard methods (Tables 1–3). These results, together with simulations that show that the combination of equations (1) and (2) yield the prescribed

false detection rates (α) (Botsford and Wainwright unpubl.), imply that this correction for intraseries correlation or a similar one should be used in correlation analysis.

Deconvolution also reduced the number of significant correlations. For example, at the 0.10 level, using the standard test, there were only 6 significant correlations with deconvolved variables, whereas there were 21 significant correlations for corresponding variables that were not deconvolved. The fact that this ratio is lower when the more conservative correlated series test is used (5 with deconvolution and 13 without) is to be expected because the test itself accounts for some of the intraseries correlation. Although the number of significant correlations is less with deconvolution, we cannot recommend its use in all situations. Deconvolution can have two positive effects on correlation analysis: (1) It can provide a better estimate of recruitment, and (2) it can reduce intraseries correlation, hence the variance of the estimate of correlation coefficient (Kope and Botsford 1988). However it can also have a negative effect. If the deconvolution is marginally stable, the abundance data is noisy, or the coefficients of the deconvolution are inaccurate, deconvolution can lead to a poorer estimate of recruitment. In the results presented here, deconvolution introduced some additional significant correlations and reduced the magnitude of existing correlations (although they remained significant at the same level). This suggests that the deconvolved series may be a poorer proxy for recruitment than the raw abundance series, and that this detracts from the removal of intraseries correlation.

The practical implication for chinook salmon managers of the correlations obtained here is primarily a recommendation of where to focus further research rather than a means of immediately achieving a dramatic improvement in management. Because these stocks are managed by annually attempting to control effort based on an attempt to predict abundance, an understanding of the factors affecting abundance is necessary. The relationship between salmon populations and oceanographic conditions during the third year has an R^2 of 0.23, and hence would not produce predictions that could substantially improve catch. It also does not hold for oceanographic conditions in the previous 3-month period, hence there is little potential for long-term prediction. However, the results do indicate two potentially useful relationships between environment and abundance. Our understanding of these relationships could possibly be improved to the point that they could be useful in management. The ability to estimate numbers at each age in catch and escapement would improve our ability to determine potential oceanographic effects as well as provide a possible predictor of catch (i.e., 2-year olds). The current practice of differentiating jacks from older fish on the basis of size leads to considerable uncertainty that could be removed by determining age through hard parts or separation of modes in the size distributions each year. Also, the existence of a demonstrated freshwater effect implies we should attempt to remove that effect from the data before searching for an oceanographic effect. However, this is complicated by the fact that an unknown fraction of the annual catch is produced by hatchery fish that were trucked below the delta for release, and hence not exposed to that effect. Better knowledge of where and when fish are released could provide the basis for removal of the effects of variable release numbers and release strategies from the data before searching for oceanographic effects.

In general, results from correlation analyses in fisheries will always contain an element of doubt and, by themselves, are probably not strong enough evidence of causal relationships that management should be based on them. Poor performance of past relationships argue for less dependence on them (Sissenwine 1984, Drinkwater and Myers 1987, Walters and Collie 1988), however, as we have shown here, there are ways of improving the reliability of correlation analyses. For example, smoothing with moving averages should be done only when the level of measurement noise warrants it, and it should always be accompanied by some means of accounting for the intraseries correlation introduced. Although we agree that the resulting statistical relationships do not, by themselves, provide a solid basis for management, we are not as pessimistic as some others (e.g., Walters and Collie 1988) regarding the utility of correlation analysis. It supplies information on patterns that allows formulation of hypotheses that can then be tested through direct means. It increases the probability of detection of relationships that might otherwise be missed. Fisheries analysts cannot afford to dismiss the opportunities it provides, but should use it only as exploratory analysis (cf. Bakun 1990, Botsford et al. 1989).

Acknowledgments

We thank L.B. Boydstun. and Chuck Knutson of the California Department of Fish and Game, D. Cayan of Scripps Institution of Oceanography, and A. Bakun of the National Marine Fisheries Service for their assistance in obtaining data. This work was supported in part by the NOAA, National Sea Grant College Program, Department of Commerce, under grant number NA80AA-D-00120, Project number R/MA-16, through the California Sea Grant College Program.

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Abstract.—Between 1980 and 1987 in Massachusetts Bay, 156 individual fin whales *Balaenoptera physalus* were photographically identified using variations in natural markings and scars. Of these, 98 (62.8%) were observed more than once, and 70 (44.9%) were photographed in 2 to 8 different years. On average, 49.2% of whales seen in a year were resighted at least once during that year, and 44.5% were observed the following year. Within a year, the observed occupancies (the period between first and last sighting) of resighted individuals varied from 1 to 197 days (mean 46.1), while the number of separate days on which individuals were sighted ranged from 1 to 12 days (mean 2.5). However, given the strong bias in photographic effort towards other species in the region, it is likely that rates of within-season occurrence and annual return are considerably underrepresented in the data. Overall, the results suggest some similarity between the population characteristics of fin whales and those of the sympatric humpback whale *Megaptera novaeangliae*, although data from whaling catches and from radio telemetry point to the existence of major differences between the two species.

Manuscript accepted 11 December 1989.
Fishery Bulletin, U.S. 88:271–278.

Population Characteristics of Individually Identified Fin Whales *Balaenoptera physalus* in Massachusetts Bay

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In recent years, techniques for the identification of individual cetaceans using variations in natural markings and scars have permitted investigations of the biology and behavior of many species (recently summarized in Hammond et al. 1990). Some of these studies have yielded detailed descriptions of the structure and patterns of migratory movement of some populations. Until recently, similar studies of fin whales *Balaenoptera physalus* had been hampered by the lack of a technique with which to reliably identify individual whales, and by the tendency of observers to concentrate on more accessible species whose ranges overlap that of the fin whale.

As a result, the high-latitude distribution of the fin whale remains poorly understood despite extensive hunting this century. On the one hand, whaling data and information from some radio telemetry studies have shown that fin whales sometimes undertake extensive movements. For example, a whale radio-tagged by Watkins et al. (1984) travelled 1700 km across the Irminger Sea in 9.5 days. Discovery tag returns suggest that Antarctic fin whales, at least over the course of several seasons, may have high-latitude ranges that encompass as much as 90 degrees of longitude (Brown 1962). In contrast to this, a whale tagged by Watkins et al. (1981) in Prince William Sound, Alaska, exhibited short-term site fidelity, remaining in a restricted area for at least 28 days. At a broader level, whaling data led Sergeant (1977) to characterize the composition of the North Atlantic fin whale population as a "patchy continuum." Mitchell (1974) believed that some spatial separation of stocks existed, but that different populations moved latitudinally with the seasons, with some whales moving south in winter to occupy the summering areas of others. Data from CeTAP (1982) generally support this idea of a seasonal shift in the population.

Mayo (1982) and Mayo et al. (1985) presented a technique for the identification of individual fin whales using variations in natural features as well as prominent scars. This technique has since been adopted by a number of observers in the western North Atlantic (Clapham 1987, Agler et al. 1990), and has been used by us to study the population characteristics of fin whales observed in Massachusetts Bay during the period 1980–87. We present here the results of this study, including evidence that fin whales on a high-latitude feeding ground exhibit patterns of seasonal occurrence and annual return that are in some respects similar to those shown for humpback whales *Megaptera novaeangliae*.

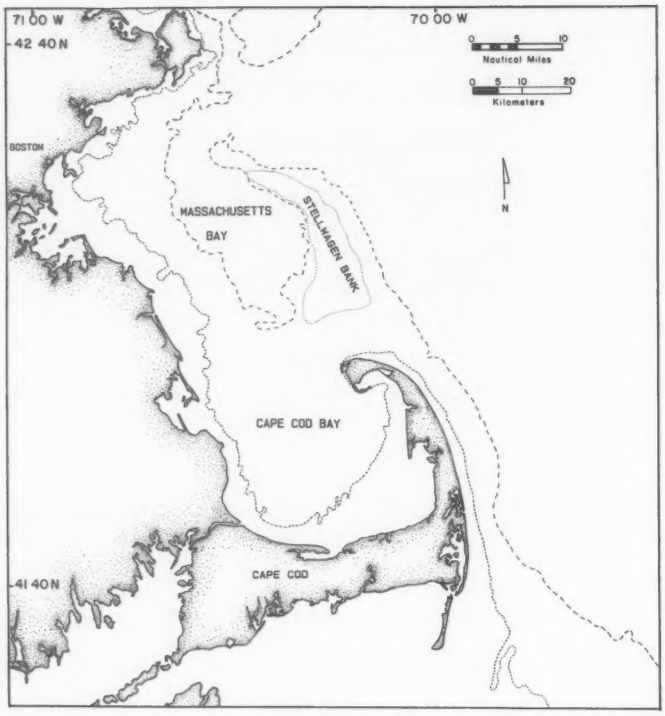

Figure 1
Fin whale study area.

Methods

The observations in this study were conducted in the coastal region dominated by Massachusetts Bay and Cape Cod Bay (Fig. 1) between the years 1980 and 1987 inclusive. Observations were made from 30-m commercial whalewatching vessels operating between April and October of each year from Provincetown, Massachusetts. Beginning in the autumn of 1983, additional cruises were made from a 12-m diesel-powered research vessel and, beginning in the autumn of 1985, from a 14-m auxiliary ketch. The total number of cruises conducted during the study period was 5979, 97% of which were made by whalewatching vessels.

Search patterns were in most cases non-random and non-systematic. This was particularly true of the whalewatching vessels, where search tracks were decided by the captains based upon where most whales had been seen the previous day or trip. Search effort directed specifically at fin whales varied considerably. Because humpback and (during the spring) right whales *Eubalaena glacialis* were preferred by the whalewatching vessels, opportunities to obtain usable photographs of fin whales occurred only incidentally except during periods when the preferred species were less abundant or absent. An exception were four fin whales that exhibited large, permanent scars that were easily noticeable from a distance of 100 m or more. Because these whales were among the few that could be readily recognized by all observers in the field, they were much more likely to be photographed, and confirmation of identity could be achieved with poorer quality photographs than those taken of unscarred whales.

Individual fin whales were identified using variations in natural markings, as described in Clapham (1987), Hawvermale (1987), and Agler et al. (1990). Major features used included the shape of the dorsal fin, the light-colored wash of pigment on the right side of the head (the "blaze"), and the V-shaped pattern of light pigment behind the blowholes and extending down both sides of the whale (the "chevron"). Scars were also used. A full definition of features and a description of the technique can be found in Agler et al. (1990).

Fin whales exhibit asymmetry in their coloration, with greater variability in features on the right side of the head than the left; consequently, while some whales were identified using both right and left sides, an individual was not considered matchable if only the

left side was photographed. Because fin whales generally have less marked variations in their features than do humpback or right whales, and because a series of photographs of high quality are generally required to successfully identify an individual, we adopted a conservative approach in our matching: only photos of excellent quality were used, and a match was considered confirmed only if three features were common in photographs of both sightings.

Photographs were taken with a 35-mm camera equipped with a 200-mm, 300-mm or 400-mm lens, power winder, and recording databack. Kodak Tri-X or T-Max film (both rated at ISO 400) was used. Copies of photographs were sent to the North Atlantic Fin Whale Catalogue at College of the Atlantic in Bar Harbor, Maine, for analysis of the movement of individual whales outside our study area.

Definitions

The following terms are used in this report:

Occupancy The sum of the resighting intervals of an individual whale within years, i.e., the number of days between the first and last sighting of a whale in a particular year. We do not assume that an individual was necessarily present in the study area for all or part of the period between sightings.

Occurrence The temporal distribution of an individual whale in the study area, expressed as the total number of separate days on which the whale was observed.

Resighting Interval The interval, in days, between successive sightings of an individual whale within a particular year.

Results

During the period 1980–87, a total of 156 fin whales were individually identified. While many other animals were photographed, this number represents only those whales that were sufficiently well-marked and well-photographed to ensure that the file contained no duplicates. A total of 98 individuals (62.8%) were observed more than once, 70 (44.9%) of which were photographed in more than one year. The photographs shown in Figure 2 provide one example of the features used to identify an individual whale in two different years.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

While fin whales were sometimes observed between the beginning of November and the end of February, none were photographed during this period in any year. (In 1979, only two fin whales were photographed, both of which were subsequently resighted).

Table 1 shows the number of individuals observed for each year of the study period, the percentage of these animals that were photographed on more than one day in that year, and that were reidentified in each subsequent year. The occurrence of identified fin whales during 1987 (the year with the largest number of cruises) is shown in Figure 3. This temporal distribution is broadly representative of other years with a similar level of effort. Table 2 summarizes resighting intervals, grouped by 10-day periods, for 1985, 1986 and 1987 combined (the 3 years with the greatest vessel effort).

Occupancy was calculated for each whale that had been observed more than once in a year (individuals seen only once or not at all in the year were excluded). Observed occupancies (n = 159, including two or more occupancy periods for individuals who were resighted in more than one year) ranged from 1 to 197 days (mean 46.1 days, SD 47.407). The mean number of days in a year that individual fin whales were photographed (occurrence) was calculated (including individuals observed on only one day, but excluding individuals not observed in the year). Observed values (n = 264) ranged from 1 to 12 days (mean 2.5 days, SD 2.011).

Of the 70 individual fin whales photographed in more than one year, 26 were observed in 2 years, 15 in 3 years, 14 in 4 years, 7 in 5 years, 3 in 6 years, 3 in 7 years, and 2 in 8 years. (These figures include the two individuals identified in 1979.) Table 3 summarizes the sighting histories of these whales.

Discussion

A major problem confounding interpretation of the data presented here is the relatively low level of effort involved in this study. An appreciation of the difference in effort directed at fin whales and at humpback whales (the whalewatching vessels' preferred species) can be gained by comparing the respective ratios of sightings to individual identifications, i.e., the total number of whales recorded (whether photographed or not) versus the number of sightings for which not only was a photograph taken, but where the photograph was good enough to positively identify the individual. For humpback whales, this ratio is consistently about 1.2:1 for all years. For fin whales, however, the ratio ranged from 11:1 in 1986 (a year with unusually low numbers of humpback whales) to 83:1 in 1981. The mean for all years was 32:1. These ratios reflect two factors. Firstly, far fewer fin whales were approached than hump-

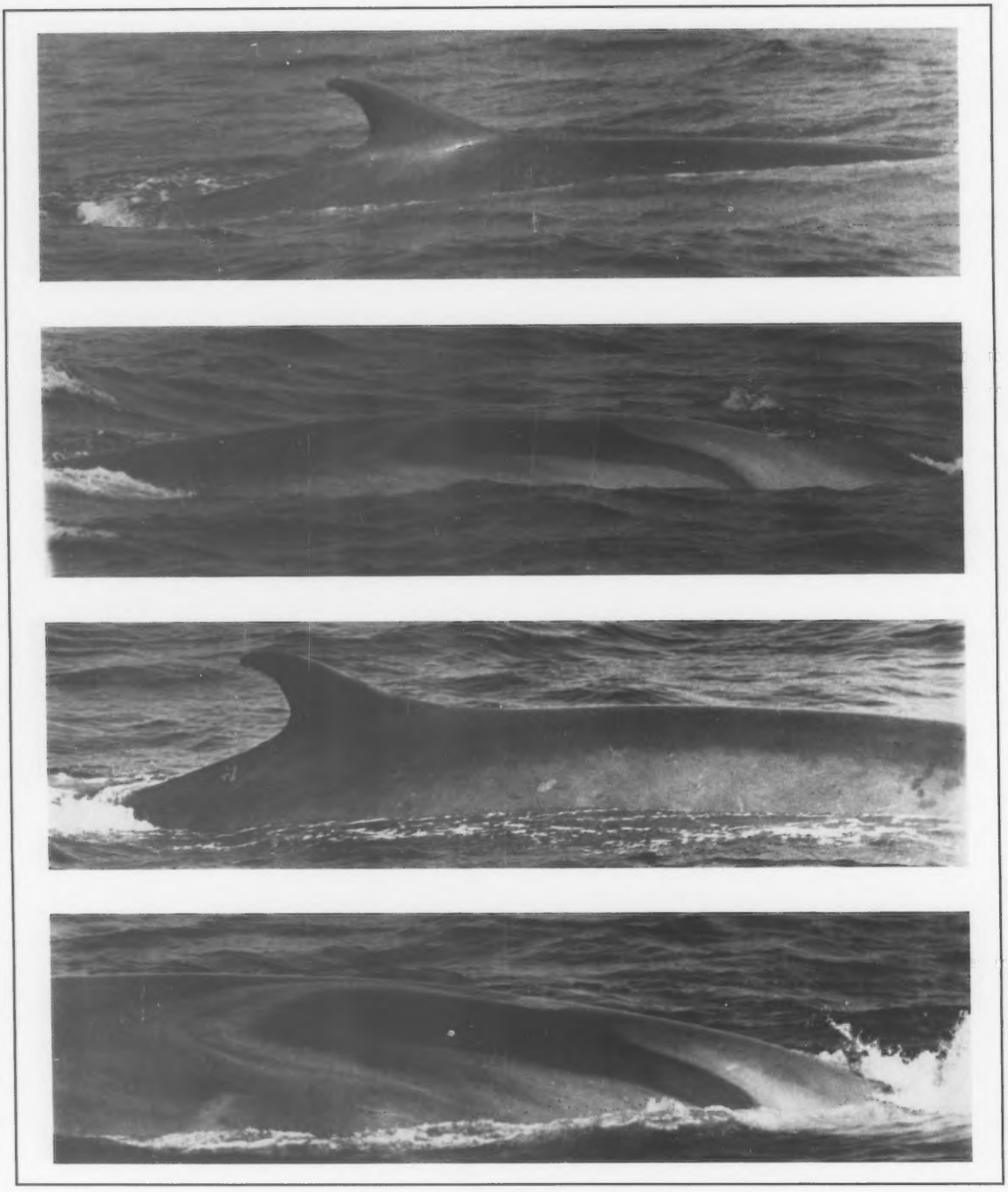

Figure 2

An example of a year-to-year match of an individual fin whale in Massachusetts Bay. The photos show catalogue number 0143 in 1983 (top two photos) and in 1987 (bottom two photos).

Table 1

The number of individual fin whales (n) identified in Massachusetts Bay for each year of the study period, and the percentage of those individuals that were reidentified within the same year, and in each subsequent year. For example, of the 22 individuals identified in 1981, 50.0% were seen more than once that year, 59.1% were reidentified in 1982, and 50% in 1983. The mean of all same-year resightings is 49.2%. The mean of all consecutive year values (e.g., 1980–81, 1981–82) is 44.5%.

	1980	1981	1982	1983	1984	1985	1986	1987
1980 $n = 21$	33.3%	38.9%	38.9%	50.0%	44.4%	33.3%	66.7%	61.1%
1981 $n = 22$		50.0%	59.1%	50.0%	40.9%	45.5%	40.9%	45.5%
1982 $n = 38$			42.1%	42.1%	39.5%	42.1%	47.4%	47.4%
1983 $n = 33$				48.5%	42.4%	36.4%	54.5%	60.6%
1984 $n = 38$					50.0%	36.8%	44.7%	50.0%
1985 $n = 31$						58.1%	54.8%	51.6%
1986 $n = 67$							52.2%	37.3%
1987 $n = 64$								59.0%

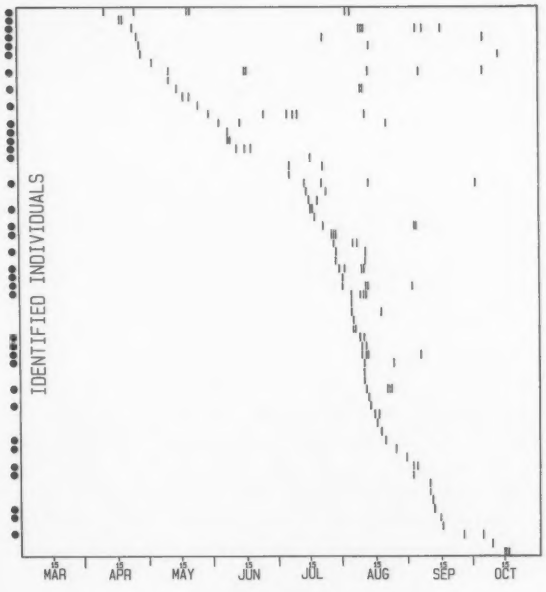

Figure 3

Observed temporal occurrence of individual fin whales in Massachusetts Bay during 1987. Individual whales are ordered (top to bottom) by date of first sighting; each row of marks represents the dates on which one individual was seen during the year. A black dot to the left of the vertical axis signifies that the individual concerned had been observed in at least one previous year of the study period.

Table 2

Resighting intervals, grouped by 10-day periods, of individual fin whales photographed in Massachusetts Bay for the three years 1985, 1986 and 1987 combined. The zero-interval category encompasses whales that were observed only once during a year.

Interval (days)	No. of intervals
0	81
1–10	146
11–20	24
21–30	14
31–40	9
41–50	6
51–60	4
61–70	2
71–80	2
81–90	2
91–100	2
101–110	0
111–120	0
121–130	0
131–140	0
141–150	0
151–160	1
161–170	1
171–180	1

Table 3

Sighting histories of individual fin whales observed in Massachusetts Bay in more than one year of the study. O = observed. Note: 0180 and 0394 were also observed in 1979.

No.	1980	1981	1982	1983	1984	1985	1986	1987	No.	1980	1981	1982	1983	1984	1985	1986	1987
0017	O	O	O	O		O	O	O	0227			O	O			O	
0027	O	O	O	O	O	O		O	0228			O	O			O	
0045	O					O	O		0230			O		O			
0061	O	O		O			O	O	0232			O				O	
0062		O	O			O	O		0233			O		O	O		O
0064	O				O		O	O	0241			O	O				O
0068	O		O						0261	O		O				O	O
0069	O			O				O	0266			O		O	O		
0081	O	O	O	O	O	O	O	O	0267			O	O		O	O	O
0086	O			O	O			O	0275			O			O	O	O
0089	O	O		O	O	O	O	O	0281			O		O		O	O
0090		O	O						0286			O					O
0093	O		O		O		O		0287				O	O			
0096	O							O	0299				O		O		
0110	O	O							0303				O		O	O	
0113				O			O		0318				O	O			
0114	O					O	O		0319				O	O		O	O
0126		O	O		O	O			0322				O	O		O	O
0131		O					O		0334				O			O	O
0137	O				O		O		0357					O		O	
0141		O	O						0367					O	O	O	O
0143		O	O	O			O	O	0391					O		O	O
0146		O	O	O	O	O		O	0394					O	O	O	O
0174		O	O		O	O			0420					O		O	
0179	O	O		O			O		0434					O		O	
0180		O	O	O	O	O	O	O	0443					O		O	O
0183		O	O	O	O			O	0452					O	O		
0189		O	O	O	O	O		O	0512						O	O	
0213			O	O		O	O	O	0520						O	O	O
0215			O	O	O	O		O	0521						O		O
0218			O		O				0542						O	O	
0222	O		O	O	O		O	O	0575							O	O
0224			O				O		0582							O	O
0225			O			O	O		0584							O	O
0226			O	O			O		0592							O	O

backs. Furthermore, while a humpback can often be recognized from a single poor-quality photograph, identification of most individual fin whales requires a series of high-quality photographs which must be taken from approximately the same position relative to the whale.

Despite this, the frequency with which individual fin whales were resighted is high. Roughly half of the fin whales seen in one year were seen again the same season, and about half were also resighted the following year. Resighting intervals provide some evidence for a degree of residency on the part of some whales, and of bimodal occupancy by others. However, the many gaps in the sighting histories of individuals are difficult to interpret. Do the gaps represent whales that were resident in the area for extended periods but were not photographed, or do they indicate movement to other areas between sightings? At this point, we can say only that, given the obvious bias in effort, it seems likely that rates of within-season occurrence and annual return of fin whales in Massachusetts Bay are considerably under-represented in our data. When only 1 out of every 83 fin whales sighted is identified (as occurred in 1981), it is unlikely that even an individual which remained in the area for many weeks would be recaptured more than a few times. This is supported by the fact that the subset of individuals towards which there was clear observer bias—those bearing large, prominent scars—were among the most frequently observed animals during this study. For example, whale number 0081, named "Braid" (an animal with very large propeller scars on its left side), was observed in all 8 years, with a mean occupancy of 116 days, and mean occurrence of 6 days.

It is clear, however, that many of the gaps in our sighting histories of individual whales represent real absences from the area. Resightings of individuals outside our study area confirm that the summer ranges of these whales are often, if not regularly, extensive. In a preliminary analysis of photographs from the North Atlantic Fin Whale Catalogue, Agler et al. (1990) report a number of instances of movement of individuals between Massachusetts Bay and the waters of Maine and the Bay of Fundy. It is possible that some individuals undertake extensive movements outside the Gulf of Maine, but the current lack of observer effort beyond this region precludes investigation of this idea.

From the regional perspective of this study, it is tempting to compare the results reported here with the much more complete information available on Gulf of Maine humpback whales and to conclude that the two populations are broadly similar in their patterns of occurrence and distribution. The annual return rate of humpback whales to Massachusetts Bay is extremely high, with as many as 85% of individuals observed in one year returning the next (Mayo 1983, Mayo et al. 1988). While no individual humpback remains in Massachusetts Bay for an entire season, many appear to spend prolonged periods in the area between making wider forays elsewhere in the Gulf of Maine (Clapham and Mayo 1987, Mayo et al. 1988). Other humpbacks are observed less often, and presumably frequent other habitats for much of the year, a fact which reflects considerable variation among individuals. It is also clear that overall individual fidelity to the Gulf of Maine is maternally directed (Clapham and Mayo 1987).

It is not unreasonable to expect that fin whales might exhibit similar patterns of occurrence. Given that the distribution of fin and humpback whales in high latitudes must be predominantly related to the distribution of their prey (Payne et al. 1986), it is to be expected that the occurrence of both species should be characterized by individuals returning repeatedly, both during a season and from year to year, to consistently productive habitats such as Massachusetts Bay. From the standpoint of energetics, it would make little sense for an individual to abandon an area of high productivity and search elsewhere if the resources found in the former habitat were adequate for its needs, although it is possible that, as suggested by Watkins et al. (1984), social imperatives play an important role in the movement of individuals.

Overall, the data presented here suggest that there are more similarities than differences in the high-latitude population characteristics of humpback and fin whales, although data from other sources suggest that significant differences between the two species do exist. In addition to the above-mentioned studies which documented extensive movements on the parts of individuals (Brown 1962, Mitchell 1974, Watkins et al. 1984), other observers have noted evidence for spatial segregation by length in certain areas (Mackintosh 1942, Mitchell 1974, Rorvik et al. 1976, Sergeant 1977), a phenomenon that has not been demonstrated for humpbacks. Our own data are regional in nature and do not permit us to address these broader questions of population structure at the oceanic level. However, with increased photographic effort in other areas, studies based upon the identification of individual fin whales should provide clearer insights into the population biology of this species in the North Atlantic.

Acknowledgments

The authors are grateful to the staff of the Center for Coastal Studies who, by ignoring humpback and right whales as often as possible, helped to provide the photographic data upon which this paper is based. We also thank Bill Rossiter for additional photographs and data, and for his consistent support of fin whale studies over the years. We are grateful to the captains and crew of the Dolphin Fleet for all their assistance in the field; we are particularly indebted to Captain Aaron Avellar, who initially suggested that variations in the blaze and chevron patterns of fin whales might be useful in the recognition of individuals. The manuscript benefitted from a thoughtful review by Scott Baker. This study was funded in part by the National Marine Fisheries Service, Northeast Region, under contract number 50-EANF-6-00059. Additional support from the International Wildlife Coalition and the Seth Sprague Educational and Charitable Foundation is gratefully acknowledged.

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Carcinonemertes wickhami n. sp. (Nemertea), a Symbiotic Egg Predator from the Spiny Lobster *Panulirus interruptus* in Southern California, with Remarks on Symbiont-Host Adaptations

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Abstract.– A symbiotic nemertean worm found on spiny lobsters is described and compared with other members of the genus *Carcinonemertes*. The new species of *Carcinonemertes* has a relatively large basis, stylet, anterior and posterior proboscis chambers, and a voluminous seminal vesicle. In addition, lateral intestinal diverticula project anterior to the level of the middle proboscis chamber. These characters distinguish this species from others in the genus.

The life-history patterns of six species of *Carcinonemertes* appear related to the developmental timing of host embryogenesis. Portunid crabs with a short duration of embryogenesis are infested by the species *C. carcinophila* and *C. mitsukurii*. The worms settle only on mature female hosts; after eclosion the worms migrate to the branchial lamellae of the host where they lie dormant until the host oviposits a new clutch. Cancrid and grapsid crabs with an intermediate duration of embryogenesis are infested by the species *C. epialti* and *C. errans*. The worms settle on both sexes of crabs and are sexually transmitted to female hosts. At eclosion, the worms die or regress and migrate to the limb axillae. Lithodid crabs and panulirid lobsters with a long duration of embryogenesis are infested by *C. regicides* and *C. wickhami*. The nemerteans settle on ovigerous hosts and die or leave the host after eclosion.

Manuscript accepted 13 December 1989.
Fishery Bulletin, U.S. 88:279–287.

Nemerteans of the genus *Carcinonemertes* (Kölliker, 1845) are specialized symbionts of decapod crustaceans. Several species of *Carcinonemertes* eat the eggs of their hosts (Humes 1942, Kuris 1978, Wickham 1980, Roe 1984); and this trophic habit may be diagnostic for the genus (Wickham 1986, Wickham and Kuris 1988). Three species have been described from the west coast of North America: *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989. Nemerteans from the spiny lobster were distinct from these species in both morphology and life history. The nemertean from the spiny lobster represents the undescribed species listed by Wickham and Kuris (1985) for that host.

Here we describe the egg predator *Carcinonemertes wickhami* n. sp., from the broods of the spiny lobster *Panulirus interruptus* (Randall), from southern California. The distinctive morphological characters of the new species are discussed, and aspects of the life history of the new species are presented with those of other members of the genus.

Materials and methods

Spiny lobsters *Panulirus interruptus* were collected by University of California divers using SCUBA. Lobsters were caught by hand. Pleopods of infested female lobsters were examined macroscopically; those containing worms were excised and immediately placed in seawater. Nine ovigerous lobsters were examined in 1982, and 10 in 1988. Three of the lobsters collected in 1988 were held for 4–7 days after eclosion (postovigerous); they were then dissected and examined for worms. Particular attention was paid to the limb axillae, branchiae, and branchial chambers. Nemerteans found in the broods of lobsters were gently manipulated onto slides for measuring and photomicrography. Worms were measured with an ocular micrometer in a dissecting microscope. They were then covered with a coverslip, and various measurements of internal features were taken with an ocular micrometer in a compound microscope. Hatched nemertean larvae were examined alive. Measurements are in

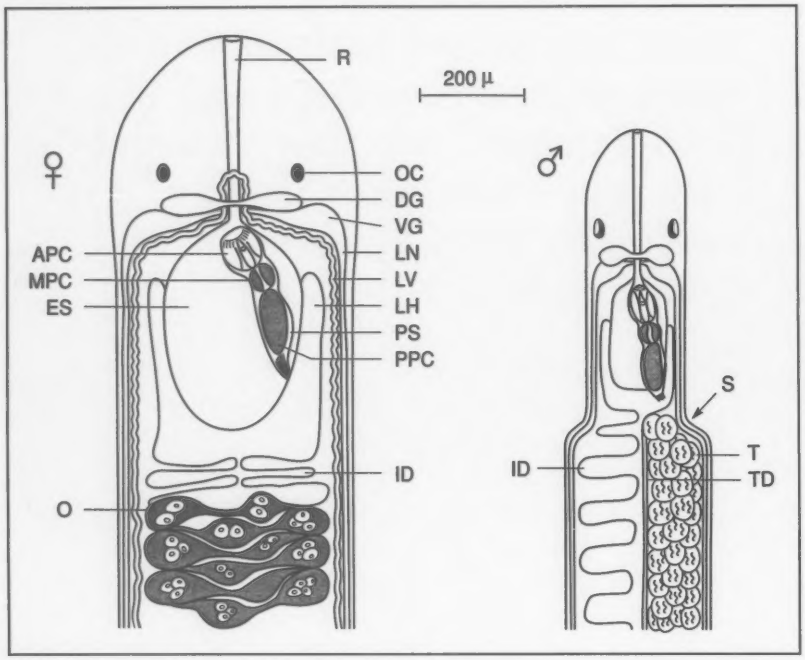

Figure 1
Composite drawing of female (left) and male (right) *Carcinonemertes wickhami* from *Panulirus interruptus*. Note the reproductive system of the male is represented on the right side of the body, while the digestive system is figured on the left side, and the circulatory system has been omitted for clarity. Key to labels: APC = anterior proboscis chamber; ES = foregut; DG = dorsal ganglia; ID = intestinal diverticula; LH = lateral horn of intestine; LN = lateral nerve cord; LV = lateral blood vessel; MPC = middle proboscis chamber; OC = ocellus; O = ovary; PPC = posterior proboscis chamber; PS = proboscis sheath; R = rhynchodaeum; S = shoulder; T = testis; TD = Takakura's duct system (vasa eferens, vas deferens, seminal vesicle, gonoduct); VG = ventral ganglion. Bar = 200 µm.

micrometers unless otherwise stated. Means are given with ranges in parentheses.

Worms were fixed in hot AFA (acetic acid, formaldehyde, alcohol) or 5% formalin-seawater. Representative specimens were sectioned at 10 µm and stained with hematoxylin and eosin.

Description

Carcinonemertes wickhami new species (Figs. 1–13)

Female (3 living specimens; 7 specimens, sectioned) Body slender, ciliated; orange color. Shape filiform with rounded anterior end, blunt posterior end; found in tough, glistening parchment-like sheaths, but often free. Sheaths with minute refractile lapilli, grainy in texture. slightly longer than accompanying worm. Worm length 10–30 mm, up to 50 mm when fully extended, average width 400 (345–456). Two ocelli anterior to prominent dorsal and ventral cerebral ganglia. Ocelli cup-shaped, conspicuous, 36 (34–39) long by 28 wide; located 145 (126–168) from anterior end. Distance between ocelli 257 (172–368). Rhynchodaeum and esophagus passing between commissures of the dorsal and ventral ganglia. Anterior portions of lateral blood vessels fuse between dorsal and ventral cephalic commissures in a single anterior loop. Posterior portion of lateral blood vessel ventral to lateral nerve cord near anus. Proboscis with three chambers, dorsomedial or lateral to posterior part of foregut. Anterior proboscis chamber 98 (84–112) long by 80 (70–87) in diameter, with basis and stylet. Basis large, 40 (36–42) long by 14 in posterior diameter. Single large stylet, 20 (19–20) long, with posterior knob-like proximal piece. Middle proboscis chamber granular in appearance, 47 (39–59) in diameter. Posterior proboscis chamber long, slender, 125 (112–140) long by 42 (28–56) in diameter; glandular, with lumen. Foregut joins rhynchodaeum at or just posterior to cephalic commissure. Posterior part of foregut robust, 380 (280–517) long, by 244 (182–345) in diameter; muscular, ciliated. Musculature of foregut attached laterally to longitudinal musculature of body wall. Posterior part of foregut leading directly into intestine; pyloric stomach absent. Intestine with a pair of lateral diverticula extending anterior to level of middle proboscis chamber. Intestine posterior to foregut with numerous paired, unbranched diverticula. Anus terminal. Ovaries elongate, with medial and lateral lobes; numerous, regularly distributed between intestinal diverticula. Ovaries with indistinct ovarian pores. Ovarian field begins immediately posterior to posterior part of foregut, extends to near anus. In section, ovaries with appearance of four rows in immature and mature females (compare Figure 4 with Figure 1); but ovaries really in two distinct rows (Fig. 1). Ovaries

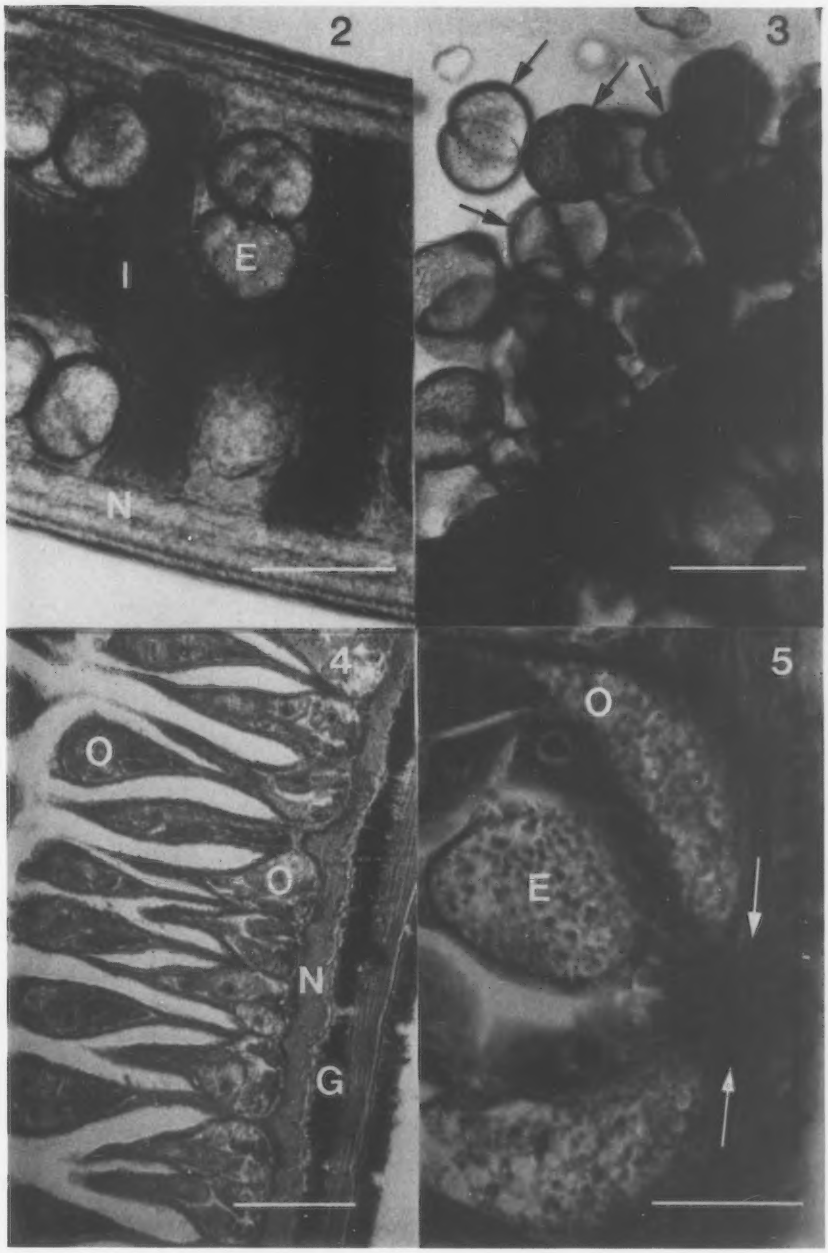

Figure 2
Fertilized embryos (E) within the ovary of a female *Carcinonemertes wickhami*; intestine (I) and lateral nerve (N). Bar = 100 μm.

Figure 3
Artificially released embryos of *Carcinonemertes wickhami*; fertilized embryos (arrows). Bar = 100 μm.

Figure 4
Sagittal section through the ovarian region of a female *Carcinonemertes wickhami*. The ovaries (O) appear in four rows but they are actually in two (only one side of worm in figure; compare with Figure 1); lateral nerve (N); submuscular glands (G). Bar = 100 μm.

Figure 5
Indistinct ovarian pore (arrows) on the lateral, submarginal surface of a female *Carcinonemertes wickhami*; egg (E); ovary (O); Bar = 50 μm.

variable in size in relation to developing ova, 196–294 long by 92–168 in diameter. Eggs faint pink, deposited in a flimsy, mucous matrix (cf. sac) secreted by female.

Male (3 living specimens, incomplete observations on 2 additional specimens) Similar in gross morphology to female; differences include: diameter of worm expands at the beginning of the testicular field, setting off the anterior portion of the worm as a relatively slender head (cf. shoulder). Color pinkish white. Ensheathed with female or free in egg mass. Length 5–18 mm, up to 20 mm when fully extended. Ocelli located

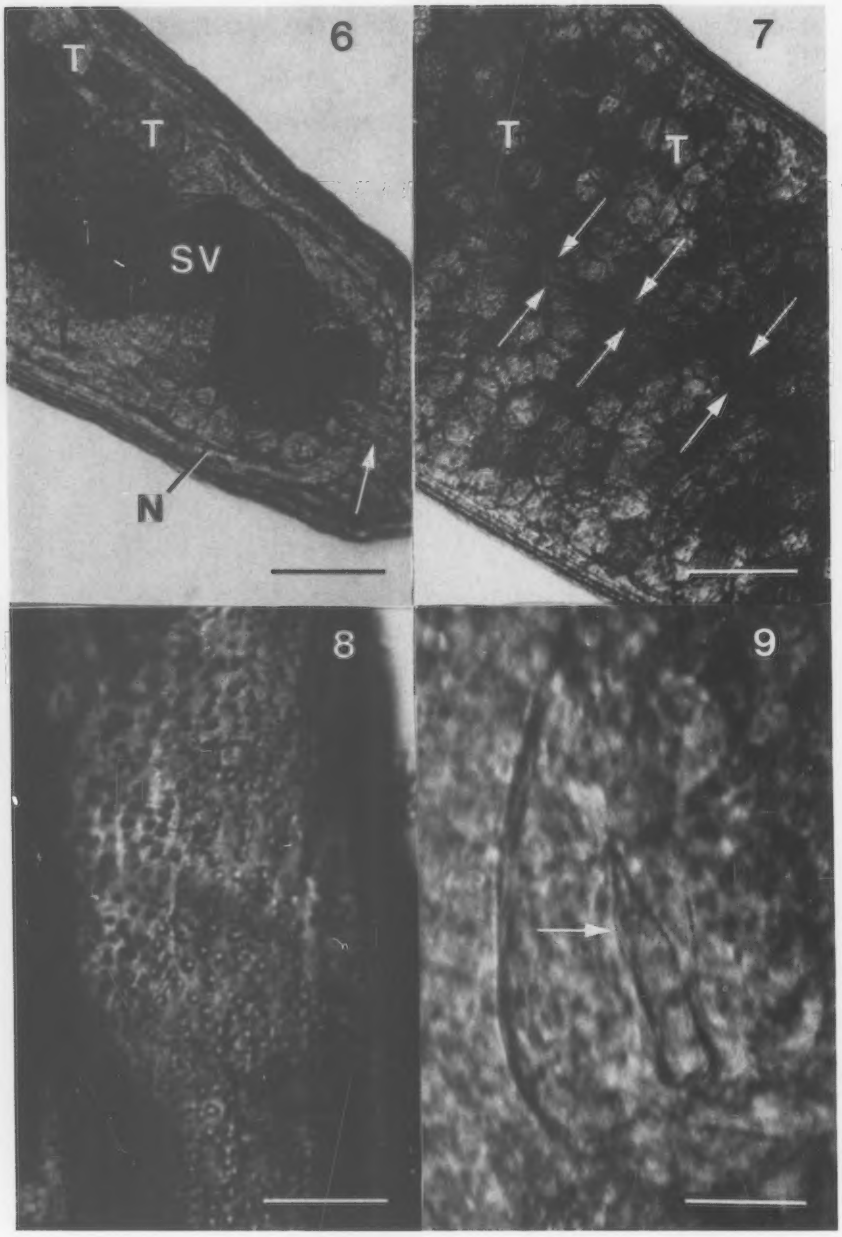

Figure 6
Posterior portion of Takakura's duct system from a live, mature male *Carcinonemertes wickhami* showing the enormous seminal vesicle (SV) and gonoduct (arrow); testis (T); lateral nerve cord (N). Note the lack of testes in the region surrounding the seminal vesicle. Bar = 100 μ.

Figure 7
Anterior portion of Takakura's duct system from a live mature male *Carcinonemertes wickhami*. The vas deferens (arrows) is distinctly visible; testis (T). Bar = 100 μm.

Figure 8
Granular, lapillated sheath of a female *Carcinonemertes wickhami*. Bar = 50 μm.

Figure 9
Stylet (arrow) and basis of *Carcinonemertes wickhami* lying in the anterior proboscis chamber. Bar = 25 μ.

163 (126–196) from anterior end; distance between ocelli 162 (151–182). Anterior proboscis chamber 79 (70–84) long by 57 (56–59) in diameter. Posterior proboscis chamber 149 (112–196) long by 47 (42–56) in diameter. Posterior part of foregut 196 (168–252) long by 151 (112–196) in diameter. Testicular field begins immediately posterior to posterior portion of foregut, extends posteriorly to terminate 659 (632–690) from cloaca. Testes located between intestinal diverticula; not found adjacent to proximal portion of the seminal vesicle. Mature testes with striated appearance, ovoid, 60 (56–70) long by 52 (42–62) in diameter. Takakura's

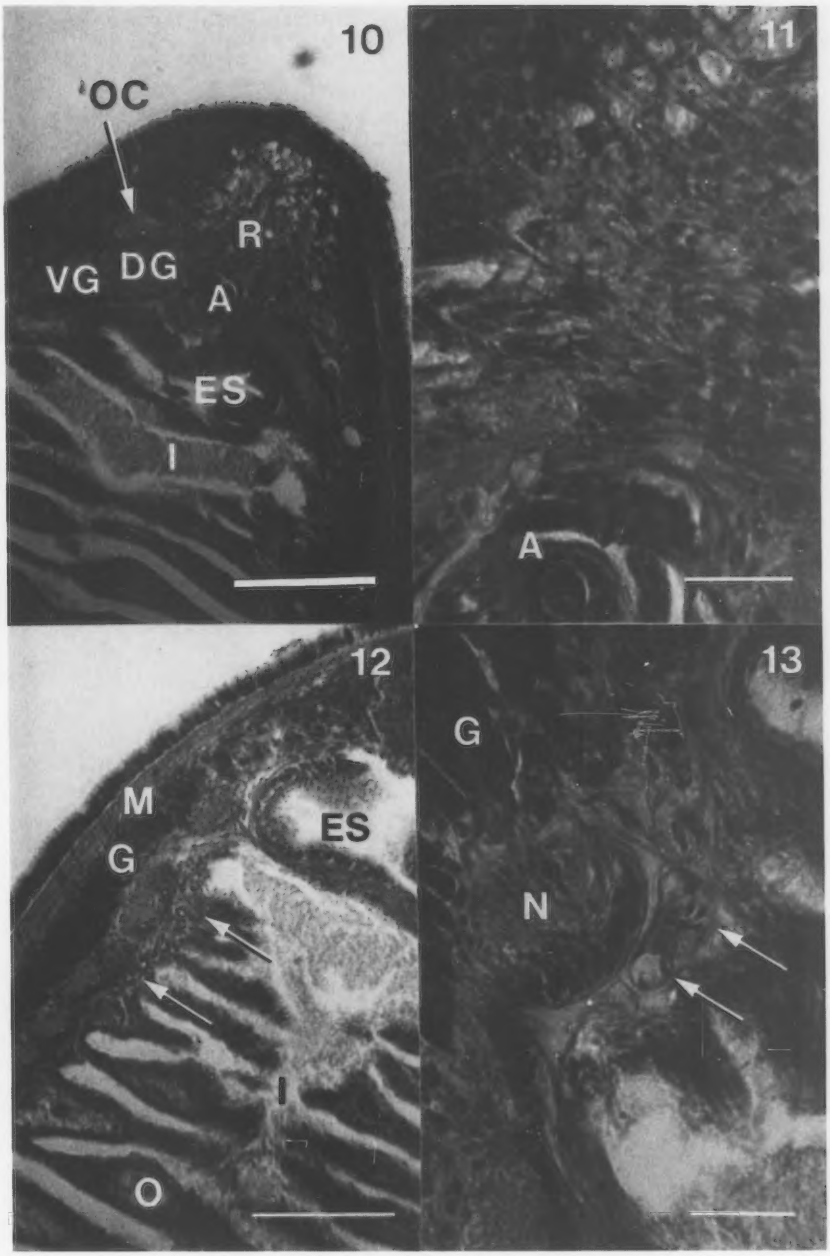

Figure 10
Sagittal section of the anterior end of a female *Carcinonemertes wickhami*; anterior proboscis chamber (A); ventral portion of the dorsal ganglion (DG); foregut (ES); intestine (I); ocellus (OC); rhynchodaeum (R); and ventral ganglion (VG). Bar = 100 μm.

Figure 11
Detail of the cephalic region of *Carcinonemertes wickhami* in sagittal section. Note the criss-crossing of the cephalic musculature; anterior proboscis chamber (A). Bar = 25 μm.

Figure 12
Sagittal section through the anterolateral portion of a female *Carcinonemertes wickhami*. Lateral blood vessels (arrows; see also Figure 13); foregut (ES); prominent submuscular glands (G); intestine (I) with intestinal diverticula; muscle layer (M) with longitudinal and circular muscles; and ovary (O). Bar = 100 μm.

Figure 13
Detail of the lateral blood vessels (from Figure 12) in the weakly developed parenchyma anastomosing between the intestinal diverticula (right) and the lateral nerve (N); submuscular gland (G). Bar = 25 μm.

duct system distinct, extending from anteromost testes to gonopore. Seminal vesicle single, voluminous, near posterior end, 421 (402–460) long by 96 (58–115) in diameter, "S" or "double-S" shape in appearance, surrounded by thick muscular region (= ejaculatory muscles?). Anus and gonoduct empty into common, ciliated cloaca with muscular sphincter.

Larvae (based on 5 living specimens) Typical hoplonemertean. Body completely ciliated, color white with

pink anterior. Larva spherical or ovoid, length approximately 84 (74–92). Anterior and posterior cirri or tufts, approximately 56 long. Two ocelli.

Taxonomic summary

Parasite *Carcinonemertes wickhami* (NEMERTEA: Carcinonemertidae).

Host California spiny lobster *Panulirus interruptus* (Randall). Found on 6 of 9 lobsters in July 1982, and 2 of 10 lobsters in August 1988.

Site of infestation Egg-bearing pleopods of female lobsters. Sometimes attached to bases of uropods or pleopods adjacent to the egg mass. Not found in/on branchiae, branchial chamber, arthrodial membranes, or limb apodemes of nonovigerous females. Not found on male lobsters.

Type locality CALIFORNIA: Santa Barbara, near More Mesa, depth of 5 meters.

Holotype USNM Helm. Coll. #80501: 1 slide—small female holotype in serial section (frontal); and larger female paratype in serial section. Date host collected: 7 July 1982.

Paratype USNM Helm. Coll. #80502: 1 vial—4 male worms; 1 vial—5 female worms; 1 vial—several egg strings attached to setae and eggs of host. Paratypes from two hosts. Hosts collected: More Mesa, 8 August 1988. Additional material in authors' collections.

Etymology The species is named in honor of Dr. Daniel E. Wickham for his contributions to the biology of the genus.

Definition Hoplonemertea, Monostilifera, Carcinonemertidae. Long, filiform nemerteans, up to 50 mm long by 400 μm wide. Anterior proboscis chamber large, 98 (84–112) long by 80 (70–87) in diameter in females; 79 (70–84) long by 57 (56–59) in diameter in males. Basis robust, 40 (36–42) long by 14 basal diameter. Stylet large, with posterior hub, 20 (19–20) long. Posterior proboscis chamber long, slender, 125 (112–140) long by 42 (28–56) in diameter in females; 149 (112–196) long by 47 (42–56) in diameter in males. Posterior portion of foregut large, robust, up to 517 long by 345 in diameter. Lateral intestinal diverticula extending to level of middle proboscis chamber. Worms often found in tough, lapillated, parchment-like sheath. Female with indistinct ovarian pores. Diameter of male expands as a "shoulder" at the beginning of the testicular field. Males with voluminous seminal vesicle, up to 460 long by 115 in diameter. Hoplonemertean larva, 84 (78–92) long.

Diagnosis *Carcinonemertes wickhami* most closely resembles *C. mitsukurii* Takakura, 1910, *C. carcinophila carcinophila* (Kölliker, 1845), and *C. c. imminuta* Humes, 1942 (Table 1). These four nemerteans have relatively large adult forms. *Carcinonemertes wickhami* can be distinguished from these large species by its relatively larger basis and stylet, anterior and posterior proboscis chambers, larger foregut, and the voluminous seminal vesicle in males (Table 1). *Carcinonemertes wickhami* can be distinguished from the smaller species (*C. australiensis* Campbell, Gibson et Evan, 1989; *C. coei* Humes 1942; *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989) by its larger size, relatively larger anterior and posterior proboscis chambers, the voluminous seminal vesicle in males, and by the presence of 2 rows of ovaries rather than 4 rows as in *C. coei* (Table 1).

Remarks and discussion

Humes (1942) and Wickham and Kuris (1988) have reviewed the genus *Carcinonemertes*, and Shields et al. (1989) and Campbell et al. (1989) have recently amended the family. Seven species are presently recognized, one of which contains two subspecies, *C. carcinophila carcinophila* and *C. c. imminuta* (Table 1). *Carcinonemertes wickhami* is the eighth species to be described, the second species described from a palinuran, and the first species described from southern California. It represents the undescribed species from the spiny lobster listed by Wickham and Kuris (1985).

Adult *C. wickhami* are often aligned along the tangled egg-bearing setae of the pleopods. The location of the worm along with its photonegative behavior make it difficult to observe this relatively large species in the egg mass of the lobster. Other species of *Carcinonemertes* also exhibit photonegative behavior (*C. epialti* and *C. regicides*; Shields et al. 1989).

The larger species of *Carcinonemertes* are well-muscled in comparison with the smaller species which exhibit a predominantly muco-ciliary movement (Shields et al. 1989). Active thrashing and peristaltic movements were noted in *C. wickhami*. Males were observed to form figure-8 loops by active muscular contraction. *Carcinonemertes wickhami* is also strongly adhesive, a property shared by *C. errans* and *C. regicides* but not by *C. epialti* and *C. mitsukurii* (Shields, pers. observ.).

Carcinonemertes wickhami, *C. australiensis*, and *C. regicides* have large anterior proboscis chambers,

Table 1

Morphological characteristics of the eight species of *Carcinonemertes*. APC = anterior proboscis chamber; PPC = posterior proboscis chamber. Measurements are in microns (except length which is mm) and represent means. NS = not seen.

Species	Sex	Length	Basis	Stylet	APC	PPC
C. australiensis Campbell, Gibson, et Evan, 1989	F&M	7.0	40.0	15–18	75	90 × 45
C. c. carcinophila (Kölliker, 1845)	F	70.0	25.0	9.0	NS	63 × 48
	M	20.0				
C. c. imminuta Humes, 1942	F	16.5	21.0	7.3	40–50	139 × 47
	M	8.7				
C. coei Humes, 1942	F	6.6	22.7	8.7	>32	78 × 47
	M	4.2				
C. epialti Coe, 1902	F&M	4.0–6.0	30.0	13.5	61–68	
C. epialti * (Shields, pers. observ.)	F	4.3	31.2	14.5	75	63 × 41
	M	2.2				
C. errans Wickham, 1978	F&M	4.0–6.0	35.2	11.0	>46	100 × 50
C. mitsukurii Takakura, 1910	F	30.0	27.0	8.0	48**	86 × 28**
	M	10.0				
C. regicides Shields et al., 1989	F	2.1	40.0	17.0	76	82 × 62
	M	1.6				
C. wickhami n. sp.	F	30.0	40.0	20.0	98	125 × 42
	M	10.0			79	149 × 47

*ex. *Cancer antennarius*
**Shields, pers. observ.

bases, and stylet apparatus. These species prey on large host eggs. In addition, the morphology of the stylet of *C. wickhami* is similar to that of *C. regicides* (i.e., in the form of a broad, flat dagger). The above adaptations may allow penetration of the thick outer coat of these large eggs (Wickham and Kuris 1988).

The presence of ovarian pores may be of taxonomic value to the genus. Distinct ovarian pores were not observed on female *C. wickhami*. Similarly, Stricker (1986) did not find distinct ovarian pores on *C. epialti*. Takakura (1910) and Shields et al. (1989) reported distinct ovarian pores from *C. mitsukurii* and *C. regicides*, respectively. The ovarian pores of *C. regicides* are typically found prior to ovulation, but are not apparent prior to oviposition (Shields et al. 1989); *C. mitsukurii* appears to follow a similar pattern (Shields, pers. observ.).

The larvae of *C. wickhami* resemble the typical hoplonemertean larval form (Gibson 1972, p. 150), and are similar to the larvae of *C. epialti* in gross morphology (Stricker and Reed 1981). Larvae most likely undergo direct development into the juvenile stage upon settling onto their host (Stricker and Reed 1981). The larva of *C. wickhami* is similar to that of *C. carcinophila*, *C. epialti*, and *C. regicides*; the larvae do, however, differ in size. *Carcinonemertes wickhami* has the smallest larva yet described for the genus.

Mature *C. wickhami* were found only in the broods of ovigerous lobsters. Further, these nemerteans have been collected only from lobsters with eggs in relatively advanced stages of development (development of eye placodes initiated—8 of 19 lobsters examined). No nemerteans were recovered from 6 lobsters with relatively early broods nor from 3 lobsters held for dissection after eclosion. *Carcinonemertes wickhami* does not appear to migrate to the branchial chamber and into the branchiae after host eclosion, nor does it move to the limb apodemes and axillae (see below).

Three distinct life-history patterns have emerged for six of the eight species of *Carcinonemertes*. These patterns appear related to the developmental timing of host embryogenesis (oviposition to eclosion): embryogenesis in various reptantian decapods can be of short (e.g., 13–16 days), moderate (e.g., 40–120 days), or long duration (e.g., 120–300+ days). In addition, life-history patterns may be useful taxonomic characters as few differences in morphology aid in distinguishing between species.

1 Portunid crabs have a short duration of embryogenesis (Churchill 1919, Sandoz and Rogers 1944). Carcinonemertid larvae settle primarily on ovigerous female crabs where they quickly metamorphose and mature. After eclosion, adult worms migrate to the

branchial chamber, encyst between the branchial lamellae, and lie dormant until the female crab oviposits (Humes 1942). Adult worms then migrate back to the clutch (Humes 1942, Hopkins 1947). Two species of *Carcinonemertes* follow this pattern: *C. carcinophila* and *C. mitsukurii*.

2 Embryogenesis of cancrid and grapsid hosts is of moderate duration (Kuris 1971, Roe 1979, Wickham 1980, Shields et al. In press). Carcinonemertid larvae settle on male and female crabs, metamorphose into juveniles, and migrate to the limb apodemes, axillae, and abdomens of their hosts. Juveniles transfer from male to female crabs during host copulation (Wickham et al. 1985). The juveniles then lie dormant, absorbing amino acids and other nutrients (Roe et al. 1982), until the host oviposits her clutch. Juvenile worms then migrate into the egg clutch and mature after eating crab eggs. Two nemerteans follow this pattern: *C. errans* and *C. epialti*.

3 Spiny lobsters and king crabs brood their eggs for long periods (Marukawa 1933; Shields, pers. observ.). Nemertean larvae settle, metamorphose, and mature only on ovigerous female crabs. Adult worms die or leave the host at eclosion. Circumstantial evidence suggests that planktonic larvae may, in at least one species (*C. regicides*), reinfect hosts immediately upon hatching (Kuris et al. In prep.). Two species follow this pattern: *C. regicides* and *C. wickhami*.

Acknowledgments

We thank UCSB divers/collectors Shane Anderson and Jim McCullough for their able collection of ovigerous lobsters. Jason Daniel Shields and Emma Ramoy provided moral support. Drs. Ian Whittington and Tom Cribb improved the manuscript. This work is a result of research sponsored in part by NOAA, National Sea Grant College Program, Department of Commerce, under grant number NA80AA-D-00120, project number R/F-75, through the California Sea Grant College Program, and in part by the California State Resources Agency. The U.S. Government is authorized to reproduce and distribute for governmental purposes.

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Age, Growth, and Reproduction of Bottlenose Dolphins *Tursiops truncatus* from the East Coast of Southern Africa

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Abstract.– Age and reproductive parameters were determined for bottlenose dolphins *Tursiops truncatus* captured in shark nets off Natal, on the southeast coast of southern Africa. Calibration of dentinal and cemental growth-layer-group (GLG) readings, using a known-age captive-born dolphin, indicated that dentinal and cemental GLGs are deposited annually, at least up to an age of 6 years. Female growth in length and mass and male growth in length are best described by von Bertalanffy growth curves. Male growth in mass is characterized by a growth spurt at puberty. Most growth occurs during the suckling years. Both sexes reach physical maturity and their asymptotic size—243 cm and 176 kg for males, and 238 cm and 160 kg for females—between 12 and 15 years. Both males and females may reach ages in excess of 40 years, based on counts of GLGs in teeth. Females attain sexual maturity between 9 and 11 years of age, 2 or 3 years earlier than males. Mating and birth are seasonally diffuse, although there is a peak of births in summer. The calf is born at a mean length and mass of 103 cm and 13.8 kg, respectively, after a gestation period of about 1 year. Lactation lasts between 18 months and two years, although there is evidence of an extended mother and calf association of up to 3 years. Postpubertal female ovulation rate is 0.28/year, and the estimated calving interval is approximately 3 years. There is no evidence that females become reproductively senescent with increasing age. Estimates of population replacement suggest that man-induced mortality may equal or exceed the replacement rate.

Manuscript accepted 6 December 1989.
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Many populations of small inshore delphinids are exploited either directly or indirectly (Mitchell 1975, Beddington et al. 1985, Northridge and Pilleri 1986), and their continued survival depends on adequate management based on knowledge of their life history. In this context, knowledge of the reproductive parameters of a species is important in formulating management and conservation proposals. In particular, the reproductive biology of females is crucial to an understanding of the likelihood of a species' survival.

An estimated 900 bottlenose dolphins *Tursiops truncatus* inhabit Natal, along a stretch of some 400 km of coastal waters, southeast of southern Africa (Ross et al. 1989). Between January 1980 and December 1987, a minimum of 212 of these animals were captured in noncommercial inshore nets set to catch and deplete the numbers of large sharks off bathing beaches (Cockcroft and Ross In press). The catch of dolphins in anti-shark nets is of concern in the continued survival of these animals off Natal (Ross et al. 1989, Cockcroft and Ross In press).

Feeding studies on the bottlenose dolphins off Natal have shown that groups are segregated by sex and size. Lactating females and their calves frequent and feed in the nearshore zone, adolescents feed slightly further offshore, while resting females and adult males feed still further offshore (Cockcroft and Ross 1990). Consequently, the catch of these animals in the shark nets is biased, with calves less than 2 years old and lactating females constituting almost 60% of the total (Cockcroft and Ross In press). Other age and sex classes, particularly pregnant females and adolescents, are, therefore, probably underrepresented.

This study was undertaken to establish the reproductive potential of bottlenose dolphins off Natal, as part of a more extensive investigation of the natural history of these animals and severity of the threat to the population through capture in shark nets. Where appropriate, recognition is given to the effects of biases in sex and size composition, noted above, which reduce the accuracy of deductions made from catch data (Perrin and Reilly 1984).

Materials and methods

Routine necropsies were performed on all bottlenose dolphins retrieved from the Natal shark nets. Biological and morphological parameters, including sex, total length, and mass were recorded for each animal, based on the recommendations of Norris (1961) and Mitchell (1975). Collected organs were preserved in 10% formalin and later transferred to 50% ethyl alcohol for storage.

Testes were excised, weighed after removal of the epididymis, and the dimensions (length × maximum height × width) measured. The epididymis was visually checked for the presence of sperm and scored as present or not; no microscopic evaluation was undertaken. Testes from young animals (combined testis mass ≲100 g) were preserved whole, while only a section removed from the bigger testis of older males was kept. Standard histological slides, approximately 5 μm thick and stained with haemotoxylin and eosin, were prepared from whole testes or from three locations (outer, middle, and inner) of sections of large testes. From each slide the diameter of a minimum of 10 circular seminiferous tubules was measured at a magnification of 125 using an ocular reticule, to assess testis development stage.

Lactating females and calves caught together were considered mother and calf pairs. Both left and right ovaries were routinely collected and preserved from all females. These were sectioned serially at about 1-mm intervals, and the number and dimensions of corpora albicantia in each ovary and the presence and dimensions of any corpus luteum were recorded. The length and mass of any fetus present in the uterus was recorded before preservation. Mammary glands were assessed for the presence of milk and, for most lactating females, the width, length, and depth measured.

The state of physical maturity of animals was assessed from the degree of fusion of the epiphyses to the centra of midthoracic vertebrae (immature = unfused, maturing = fusing, and mature = fused). The brain mass of neonates and calves was measured directly. That of adults was estimated by filling the skull with coarse dry sand, after first sealing all apertures with adhesive tape, measuring the volume of sand in a measuring cylinder, and assuming this to represent the brain mass.

Age was determined from the number of growth-layer groups (GLGs; *sensu* Perrin and Myrick 1980) counted in the dentine and cement of longitudinal thin sections of teeth. The largest mandibular or maxillary teeth were used. Numerous methods of obtaining thin sections were employed, including hand grinding on 1200-grade abrasive paper or between glass sheets using jewelers rouge, or obtaining thin (~20 μm) ground sections using a geological abrasive wheel. However, the best results were achieved with a custom-built, slow speed saw and diamond lapidary blade that cut thin (120 μm) sections. These were etched in 5% formic acid for 5 minutes, washed in running water for 1 hour and dried and mounted on perspex slides using cyanoacrylate glue. Sections were then viewed, at 8× magnification, through a binocular microscope using both transmitted polarized light and reflected light on the pencil-rubbed etched surface of the tooth.

Dentinal GLGs in all teeth were counted three times by each of two independent observers. Additionally, one observer (VGC) made a minimum of three cemental GLG counts in all teeth where the pulp was occluded, but only in a selection of teeth in which it was not. Initially, dentinal and cemental GLG counts were assessed separately, and the mean of any three counts (dentinal or cemental) that were within 15% of one another was accepted as the age of the animal. However, in teeth where counts varied by more than 15%, further counts were done until any three were within 15% of one another. Finally, for teeth where the pulp cavity was open, the mean of a combination of GLG counts in both cement and dentine was accepted as an estimate of age. Where occlusion of the pulp had occurred, only mean cemental counts were used to estimate age.

The number of dentinal and cemental GLGs in the teeth of one known-age animal ("Dolfie," PEM N6, born 30 December 1972 and died 9 August 1979) were also counted as above. In addition, because of the importance of the age estimate of this animal, a third observer (GJBR) counted GLGs in the dentine.

Results

Age and growth

More than 6½ but less than 7 dentinal GLGs were counted in teeth of the known-age animal "Dolfie" (Fig. 1). This corresponded well with the actual age of 6 years and 8 months and indicated an annual deposition of GLGs in the dentine. However, only six GLGs were counted in the cement of this animal, indicating that cemental GLGs probably reflect whole years only and may underestimate age by 1 year. Despite this, cemental and dentinal GLG counts were taken to represent age in years.

Age estimates from dentinal and cemental GLG counts of the teeth of 174 male and female *Tursiops* were well correlated ($r = 0.95$ and $r = 0.96$, respectively) up to approximately 12 GLGs; thereafter, counts diverged with increasing age due to the closure of the pulp (Fig. 2). The smallest individual from the nets was 29 kg and 125 cm, and had about 15% of the first GLG formed (2 months old). The heaviest male was 204 kg, the longest was 257 cm, and the oldest 42 years. The corresponding parameters for females were 182 kg, 249 cm, and 43 years, respectively.

The relationships of both body length and mass to age, for captured *Tursiops* and stranded or captive born neonates, were fitted to a number of growth curves, including those of Gompertz, Richards, Putter, and Schnute. However, growth with age, for both

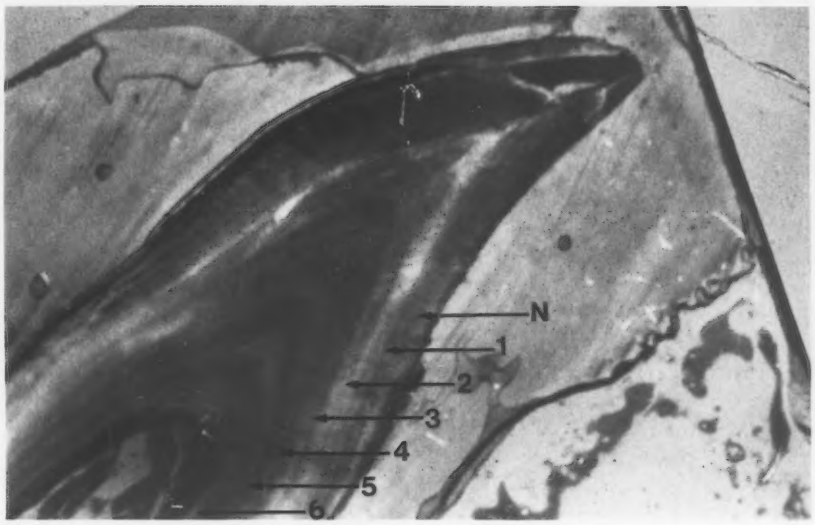

Figure 1
A thin-etched section of a tooth from "Dolfie", a captive-born bottlenose dolphin captured off southern Africa. The neonatal line (N) and the end of each of six growth-layer groups are marked.

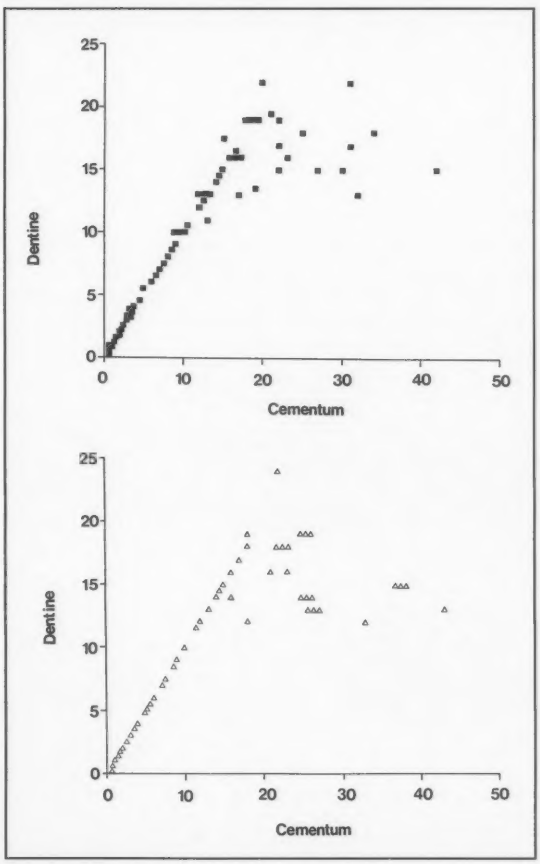

Figure 2
Relationship between growth-layer-group counts in the dentine and cement of male (■) and female (△) bottlenose dolphins captured off southern Africa.

males and females, was best defined by derived von Bertalanffy growth curves (Figs. 3,4) of the form:

$$l(t) = l_{inf}(1 - e^{-k(t-t_0)})^p$$

Asymptotic length and mass, calculated from the mean length and mass of physically mature males (243 cm and 176 kg) and females (238 cm and 160 kg), were slightly overestimated by the derived curve (Table 1), but both show that the asymptotic length and mass of males are greater than of females. There was no significant difference between the mean mass of lactating and nonlactating mature females ($t = 0.236$, $P<0.01$) which may have contributed to this sexual dimorphism.

Length and mass at birth L_{t0} predicted in Table 1 were almost identical to length and mass at birth (103 cm, range 86–115 cm, SD 7.6, $N = 26$; 13.8 kg, range 9.1–21 kg, SD 2.9, $N = 15$) calculated from the mean length and mass of captive-born or stranded neonates in which the umbilicus was unhealed.

In both males and females, most growth occurred during the first 10 to 12 years of life and thereafter reached a plateau (Figs. 3,4). In females, both mass and length increase in a smooth, continuous process with no evidence of any discontinuity. In males, length increase follows a similar pattern, whereas mass increase

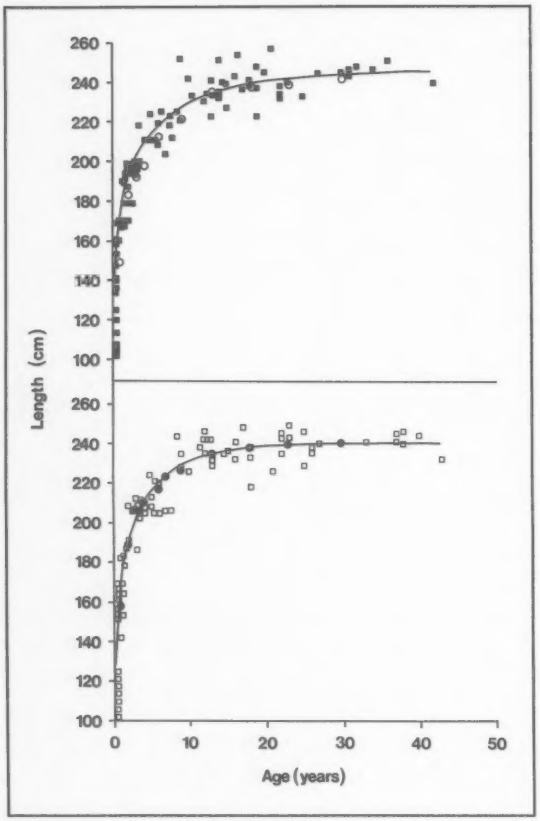

Figure 3

Increase in length with age (growth) of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data. Mean lengths for various age classes of males (○) and females (●) are also shown.

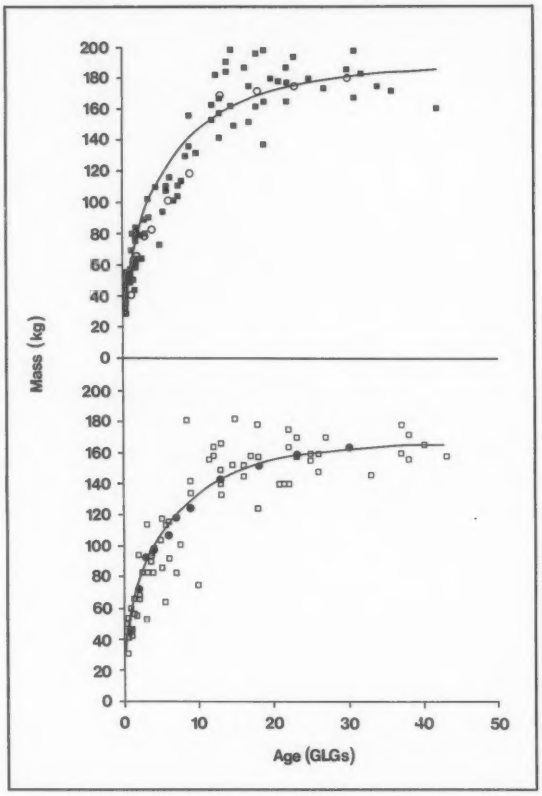

Figure 4

The increase in mass with age of male (■) and female (□) bottlenose dolphins captured off southern Africa. A four-stage von Bertalanffy growth curve is fitted to these data (see text). Mean mass for various age classes of males (○) and females (●) is also shown.

Table 1

Parameters derived from a four-stage von Bertalanffy growth curve ($L(t) = L_{inf}(1 - e^{-k(t-t_0)})^p$) fitted to age-length and age-mass data for male and female bottlenose dolphins captured off southern Africa.

	Males		Females	
Parameter	Length	Mass	Length	Mass
L_1	102.775	14.7865	102.0206	14.64186
L_2	245.016	185.217	239.9296	165.7209
t_0	−0.02261	−0.0676	−0.056844	−0.05725
L_{inf}	245.611	187.254	239.9625	166.8249
k	0.09712	0.09105	0.167249	0.099103
L_{t0}	103.4	14.9	102.3	14.8
n	100	88	88	84

L_1 = Smallest length or mass in the sample
L_2 = Largest length or mass in the sample
t_0 = Age corresponding to zero length
L_{inf} = Asymptotic length or mass
k = Constant of catabolism
p = Power constant
L_{t0} = Estimated length of mass at birth
n = Sample size

Table 2

Range in age (growth-layer-group) at which the vertebral epiphyses of male and female bottlenose dolphins captured off southern Africa were unfused, fusing, and fused.

	Unfused	Fusing	Fused
Males	0–8	4–14	>12
Females	0–6	4–13	>12

Table 3

Length, mass, and brain mass of six stranded or captive-born neonate bottlenose dolphins captured off southern Africa.

	Length (cm)	Mass (kg)	Brain mass (g)
	100	12.4	562
	105	17.7	680
	106	14.8	738
	106		595
	108	13.0	635
	109	13.4	625
Mean	106	14.3	639

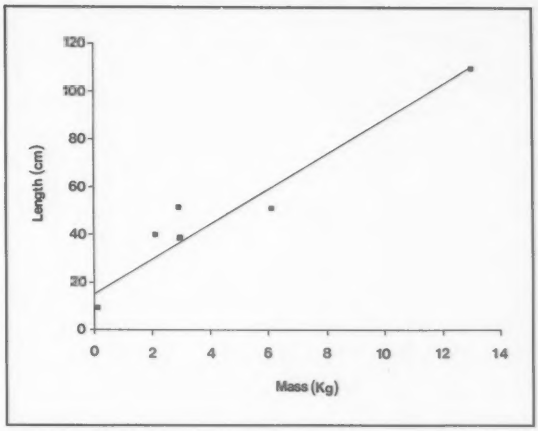

Figure 5

Fetal growth in length and mass of bottlenose dolphins captured off southern Africa, and a regression of the form (length = 23.914 + 0.006 × mass) drawn through these data.

shows a clear discontinuity between 10 and 13 years of age (Fig. 4), indicating that a two-stage growth curve may better fit these data.

The mean length and mass of the first five year-classes (calculated from calves displaying whole, completed GLGs only) showed that growth rate during the first year far exceeded that in any other. Mass increases in the first year by some 255% of mean birth mass, but increases over the subsequent 4 years slow to 49%, 13.5%, 10.6% and 3.8%, respectively. In contrast, length increase is much less rapid over this same period and is approximately 57%, 15.2%, 3.7%, 4%, and 5.5%, respectively. In both males and females the relationship between mass and length, up to asymptotic values, is well defined by power curves (males, log mass = $-5.1 + 3.06 \times$ log length, $r = 0.97$; females, log mass = $-4.7 + 2.9 \times$ log length, $r = 0.95$).

Both male and female bottlenose dolphins appear to reach physical maturity between 12 and 15 years of age (Table 2). The youngest physically mature animal was 12 years old while the oldest nonphysically mature animal was 14 years old (Table 2).

Female reproduction

Only six (2.8% of the total catch and 12% of mature females) of the captured females were pregnant, and the growth of the six fetuses—length (cm) against mass (kg)—was well defined by a linear regression (Fig. 5). Although no estimate of gestation period was possible from these data, an estimate was obtained from the relationship between neonatal and adult brain mass (Sacher and Staffeldt 1974, *in* Perrin et al. 1977). A neonatal brain mass of 639 g was estimated from the mean brain mass of six stranded or captive-born neonates in which the umbilicus was unhealed (Table 3). An asymptotic brain mass of 1460 g was calculated from the mean brain volume of physically mature females, although the variation in maximum size of females would obviously affect this. Application of the Sacher and Staffeldt equation gives a gestation period of some 372 days. An alternative method of estimating gestation period based on the relationship between birth length and gestation period (Perrin et al. 1977) yielded an estimate of 12.3 months or 374 days, assuming a birth length of 103 cm.

Birth date, to the nearest month, was back-calculated for 25 captured calves less than 1-year-old by measuring the width of deposited dentine as a proportion of the mean width of the first GLG (Fig. 6). The mean width of the first GLG layer was 279 μm ($N = 29$, range 229–331 μm) with a 95% CI of 10 μm, indicating a maximum error of about 13 days. The subtraction of age from date of capture (Fig. 6) suggests that most births occurred in summer.

In all females the majority of ovarian scars (80%) occurred in the left ovary. The maximum number of scars in any ovary was 11, with no indication that ovary mass decreased with the number of scars (Fig. 7). Age-, mass-, and length-related ovulation rates appear extremely varied in bottlenose dolphins (Fig. 8). In only one female was there one scar, so calculation of mean age at first ovulation was impossible. This 13-year-old

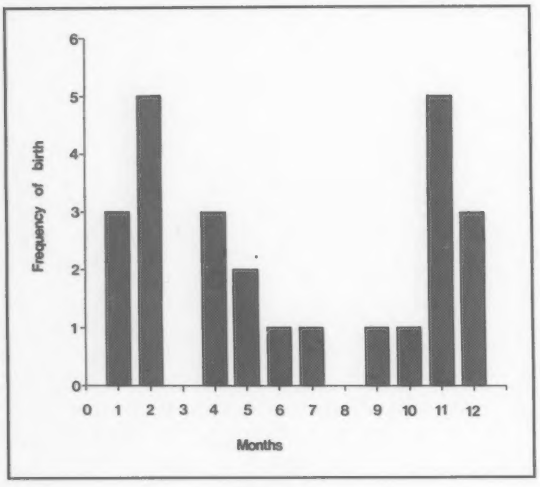

Figure 6
Birth month of 25 bottlenose dolphin calves captured off southern Africa back-calculated from the width of the first dentinal growth-layer-group.

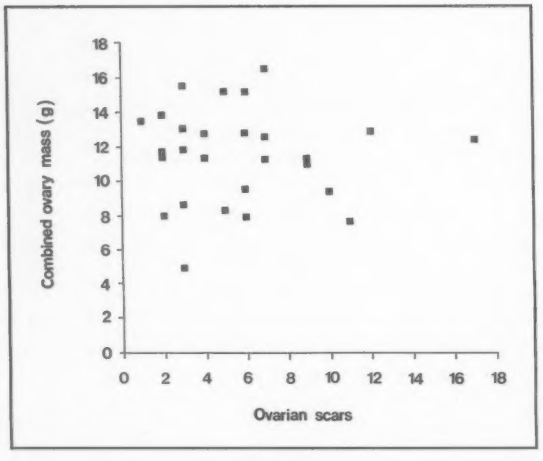

Figure 7
Relationship between combined ovary mass and the total number of ovarian scars for female bottlenose dolphins captured off southern Africa.

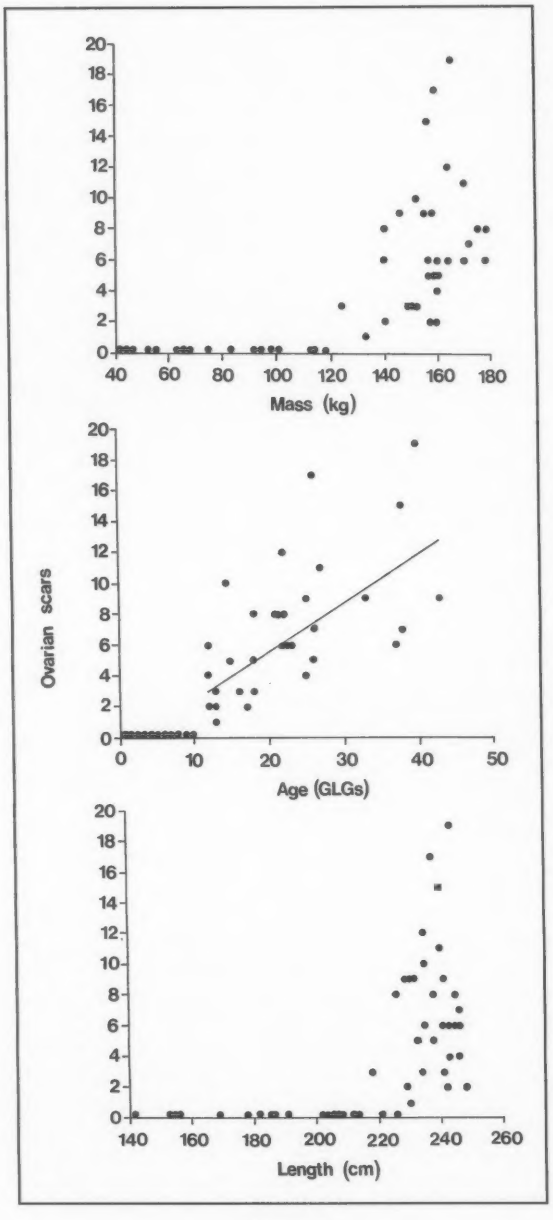

Figure 8
Increase in the number of ovarian scars with mass, age, and length of female bottlenose dolphins captured off southern Africa. A linear regression (no. ovarian scars = 0.58 − 0.29 × age) fitted to this relationship in postpubertal females is shown.

female had a *corpus albicans* measuring 10 × 8 × 8 mm (index volume 640 mm^3) and was lactating, indicating she probably had a suckling calf. Extrapolation from a regression of calf length on an index of largest corpora volume, for mother-calf pairs (Fig. 9), suggests that the calf would have been some 184 cm in length or 18 months old (Figs. 3,4), implying that her first ovulation and conception occurred at approximately 10.5 years of age.

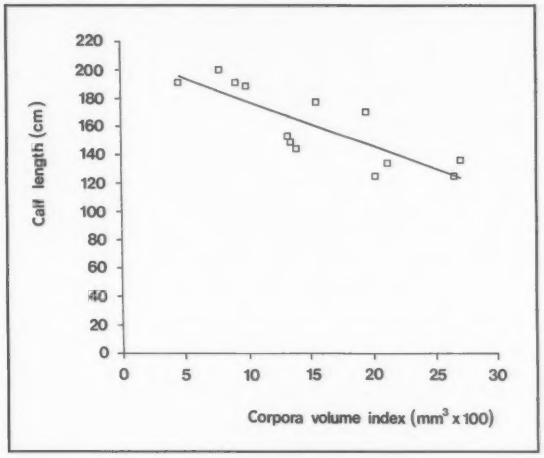

Figure 9
Relationship between the length of a bottlenose dolphin calf and an index of the volume of the most recent or largest corpus in the mother. The fit of a linear regression (calf length in cm = 209.61 − 0.032 × corpora volume index) to these data is shown.

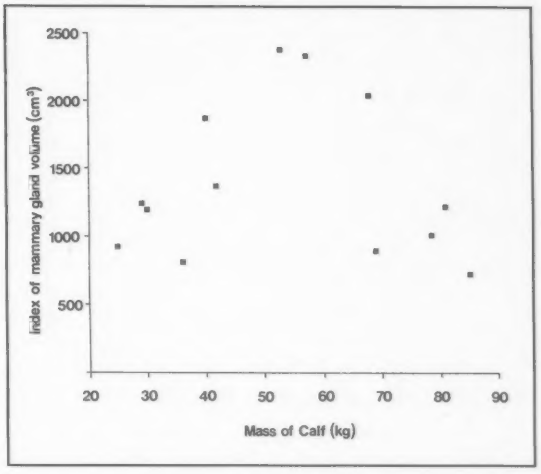

Figure 10
Relationship between the mass of a bottlenose dolphin calf and an index of the volume of the mother's mammary glands.

Two other females, 12 and 13 years old, which had each undergone two ovulations, were lactating and the index volumes of their largest *corpora albicans* were 900 mm^3 and 2100 mm^3, respectively. Extrapolation from Figure 9 suggests that the calves of these females were approximately 181 cm or 18 months old, and 143 cm or 6 months old, respectively. These data imply that at conception of the calves, these two females were about 10.5 and 9.5 years old, respectively. The above data, and the presence of 10-year-old females that had not ovulated, imply that first ovulation occurs between 9.5 and 11 years of age. One 17-year-old female had undergone two ovulations, was lactating, and had a 170-cm calf of approximately 1-year-old. This suggests that this female was 15-years-old at the time of conception of this calf, although she may have undergone a previous pregnancy.

A regression fitted to the number of ovarian scars on age of sexually mature females has a slope of 0.29 ($r = 0.6$, $N = 32$), implying that mature females, in general, ovulate at least every third year (Fig. 8). A similar regression of log of age on log of number of *corpora albicantia* was linear (log age = $-0.61 + 1.03 \cdot$ log # scars, $r = 0.62$), indicating no decrease in ovulation rate with age.

Length of lactation calculated from the catch statistics of animals on the Natal coast (Cockcroft and Ross In press) where 27% and 5.2% of females were lactating and pregnant, respectively, gave an estimate of 5.2 years (proportion lactating/proportion pregnant; Perrin and Reilly 1984). As this is obviously exaggerated by the overabundance of lactating females and dearth of pregnant females, alternative means of estimating lactation period are required. The relationship between calf mass and an index of mammary gland volume (length × height × depth) in 13 mother and calf pairs suggests that the mammary glands increase in size during lactation, until the calf's mass is between 60 and 70 kg, after which the mammary volume decreases (Fig. 10). Extrapolation from the growth curves suggests that calves of this mass are about 18-months-old. An examination of the stomach contents of captured calves and juveniles showed that solids first appear in stomachs at about 6 months of age, although milk remains were still evident in calves of up to 3 years of age.

Of the 20 known mother and calf pairs, ten calves were 1 year old or less, five were 1–2 years old and a further five were greater than 2 years old; the mother of one of the latter was pregnant with a fetus of only 38.5 g. Although only solids were found in the stomach of her 69-kg calf, she was still lactating, the only one of six pregnant females simultaneously lactating. These facts imply a mother and calf association of up to 3 years before a subsequent pregnancy.

Female resting period calculated from gestation period (1 year), proportion of females resting (5.3%) and the proportion of females pregnant (Perrin and Reilly 1984) yielded an estimate of about 1 year.

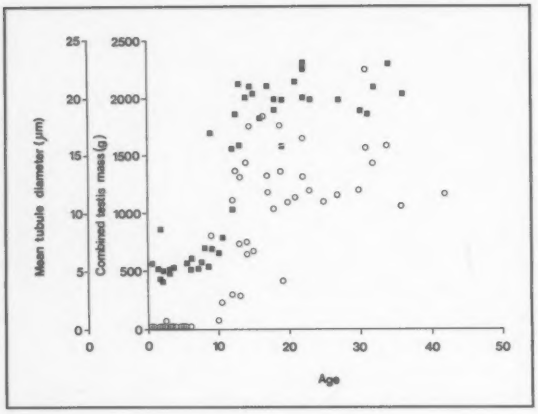

Figure 11
Increase of mean seminiferous tubule diameter (■) and combined testis mass (O) with age in male bottlenose dolphins captured off southern Africa.

Table 4
Mean age, mass, and length of male bottlenose dolphins captured off southern Africa, with testes showing no mature tubule development (stage 1), some (~half) mature tubule development (stage 2), and 75–100% of tubules mature (stage 3/4).

	Testis development stage		
	1	2	3/4
Age	4.68	14.3	20.6
Mass (kg)	90.8	151	174
Length (cm)	201	228	241
n	22	6	25

Male reproduction

No consistent differences were found between mean seminiferous tubule diameter of samples taken from the outer, middle, and inner sections of testes. In general, left and right testes were of similar mass ($r = 0.95$, $N = 46$). Combined testis mass remained low (<100 g) up to approximately 10 years of age, approximately 140 kg body mass, and a length of 225 cm, but thereafter increased rapidly (Figs. 11,12). Tubule diameter growth and state of testes development (Mitchell and Kozicki 1984) showed a similar pattern of growth with age, mass, and length (Table 4, Fig. 11), although development of tubules appeared to occur earlier than did the increase in testis mass. The maximum mature testis (stage 4) mass of any male was 1160 g and the largest apparently immature testis (stage 1) was 130 g. The smallest testis at stages 2, 3, and 4 were 140 g,

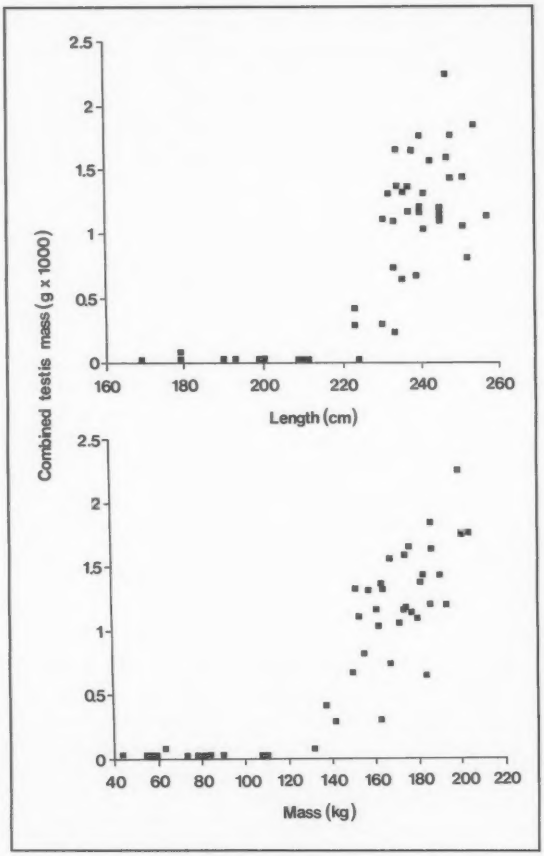

Figure 12
Increase in combined testis mass with mass and length in male bottlenose dolphins captured off southern Africa.

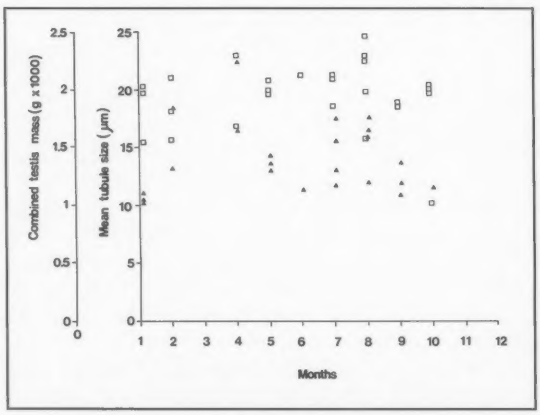

Figure 13
Influence of season (month) on combined testis mass (▲) and mean testis seminiferous tubule diameter (□) in male bottlenose dolphins captured off southern Africa.

320 g and 310 g, respectively. Mean age, mass, and length of males according to testis development stage are given in Table 4. Puberty in male *Tursiops* from the Indian Ocean may begin as early as 9 years of age but primarily between 10 and 12 years (Fig. 11). However, sexual maturity (50% each of stages 2/3 and 4) occurs only at about 14.5 years of age, a length of 240 cm and a mass of 165 kg.

There was no evidence of a seasonal pattern in either combined testis mass and tubule size (Fig. 13) or the presence of sperm in the epididymis.

Discussion

The similarity of dentinal GLG counts to "Dolfie's" actual age indicates an annual deposition of dentinal GLGs for at least the first 6 years. Ross (1984) superimposed the growth rate of this animal on a length-versus-age (dentinal GLGs) relationship in bottlenose dolphins from Natal and the Eastern Cape, and concluded that "the best fit of the points to the curve is reached when the accumulation rate of dentine layers is equal to one per year." Similarly, when the growth rate of another captive Indian Ocean animal (Cockcroft and Ross 1990b) is fitted to the curve, the relationship is best explained by an annual deposition of dentinal GLGs, also proposed for *Tursiops* in other areas (Sergeant et al. 1973, Hui 1980).

In contrast to apparently continuously deposited dentinal GLGs, cemental GLGs appear to be rapidly deposited and only accumulate as whole layers in the teeth of *Tursiops*. Nevertheless, the strong correlation between dentinal and cemental age estimates up to occlusion of the pulp cavity, and the similarity of dentinal and cemental GLG counts in teeth of the captive animal, suggest that cemental GLGs also accumulate annually and are reliable estimators of age in bottlenose dolphins from the Indian Ocean, at least up to an age of 12 years. Despite the lack of direct evidence, it seems likely that cemental GLGs are deposited annually even after 12 years.

Male and female Indian Ocean bottlenose dolphins may attain an age greater than 40 years (cf. Ross 1977) with little difference in the apparent maximum ages of the sexes. In excess of 20% of the Natal net catch were older than 20 years, indicating a long-lived species. Few data are available on the longevity of *Tursiops* elsewhere, and most existing studies have used dentinal age estimates. Sergeant et al. (1973) estimated the longevity of *Tursiops* from northeast Florida to be about 25 years, with no apparent differences in the life expectancy of males and females. Hohn (1980), in a study of *Tursiops* from the southeast coast of the United States, found animals with up to 27 dentinal GLGs, males and females reaching similar ages. In contrast, the maximum age of spotted dolphins, estimated from cemental GLGs, is in excess of 45 years (Kasuya 1976). Thus, the use of cemental GLG age estimates in future studies of bottlenose dolphins may yield greater estimates of maximum age.

The estimated mass and length at birth of Indian Ocean bottlenose dolphins in this study are comparable with those calculated by Ross (1984). Subsequent to birth, growth is rapid, particularly in terms of mass, but decreases gradually with age. The proportional length increase is similar to that previously recorded for bottlenose dolphins from Natal and the eastern Cape (Ross 1977, 1984; Cockcroft and Ross 1990b) and also those from other areas such as northeast Florida (Sergeant et al. 1973), the western North Atlantic (Hohn 1980) and captive animals from the Pacific coast of Japan (Kasuya et al. 1986). An enormous increase in mass during the first (suckling) year is well known in seals and balaenopterid whales but has not often been recorded for delphinids. Presumably, a large initial mass increase reflects the rapid development of the calf and its need to reach thermoregulatory equilibrium as well as some social and motor independence from its mother (Cockcroft and Ross 1990b) before the female's involvement with the next pregnancy and calf.

The asymptotic length and mass values obtained in this study and those of Ross (1977, 1984) are less than those for bottlenose dolphins from the western North Atlantic (Hohn 1980), Florida (Sergeant et al. 1973), and the Japanese Pacific (Kasuya et al. 1986). It is unclear why bottlenose dolphins from different areas have varying asymptotic sizes. Some authors have suggested that this may warrant the separation of the various populations to the specific level (Ross 1977), although Ross and Cockcroft (1990) have suggested that there is little morphometric evidence to suggest this and that such differences may only have resulted from environmental conditions, particularly temperature.

The asymptotic lengths of male and female Indian Ocean bottlenose dolphins are only slightly different (243 cm and 238 cm, respectively). In the western North Atlantic, Hohn (1980) found no difference in the maximum lengths of males and females. These results support the findings of Sergeant et al. (1973) that the total lengths of male and female delphinids, in general, do not appear to be different, although they found that the asymptotic length of male *Tursiops* from Florida was 20 cm greater than that of females.

In contrast, fully grown male Indian Ocean bottlenose dolphins are considerably heavier (9%) and more robust than females (176 kg and 160 kg, respectively). Lactating and nonlactating females had a similar mean mass, indicating that this mass difference cannot be

attributed to stress and blubber mass loss through lactation (Cockcroft and Ross 1990a, b). Some of this mass difference between the sexes may be a direct consequence of the male mass growth spurt between 10 and 12 years of age. It is unclear why this growth spurt is not reflected in the length of males; it may be that robusticity and not length is important in male and female interaction.

Despite this, the male growth spurt at the onset of puberty may be similar to the two-stage growth that Perrin et al. (1976, 1977) described for male and female spotted and spinner dolphins in the eastern tropical Pacific where growth showed a pubertal secondary growth spurt. In male bottlenose dolphins, this spurt occurs 4–5 years later than in spotted or spinner dolphins but also at the onset of puberty, suggesting that such growth spurts may be directly related to the attainment of sexual maturity. It is possible that this growth spurt may also be evident in female bottlenose dolphins but is not discernible owing to the small sample size.

Females mature sexually some 2 or 3 years prior to the attainment of physical maturity in contrast to males, where sexual maturity is attained just before physical maturity. In both sexes, however, physical maturity occurs almost in concert with the occlusion of the tooth pulp cavity, supporting previous suggestions that animals with occluded pulp cavities are sexually and physically mature (Ross 1977, 1984). Females attain sexual maturity at least 2 years earlier and at a lesser length and mass than do males, although the reduced number of first-time ovulators and high occurrence of females with multiple ovulations will have biased this upwards. It is not unusual for female delphinids to attain sexual maturity sometime before and at a smaller size than males. Female *Tursiops* in the western North Atlantic also appear to follow this pattern (Sergeant et al. 1973). Female spotted and spinner dolphins reach sexual maturity about 3 or 3–4 years, respectively, before males and both are smaller than their male counterparts (Perrin et al. 1976, 1977). It has been proposed that this disparity ensures more sexually mature females than males in the population (Bryden 1972). Intensive behavioral field work is needed before this suggestion can be confirmed.

Although no direct estimate of gestation period was available from the fetal growth data, both derived estimates were in excellent agreement, about 373 days. A 373-day gestation period is slightly longer than previous estimates for Indian Ocean *Tursiops*, which range from minimums of 342 and 341 days (Saayman and Tayler 1977) to maximums of 364 and 368 days (Ross 1984) in captive bottlenose dolphins. Similar estimates of the gestation period in captive *Tursiops* from other areas have been given by Tavolga and Essapian (1957), McBride and Kritzler (1951), and Kasuya (1985).

Although the sample was too small for an assessment of the age at first ovulation, the onset of ovulation in females is apparently rapid. Thereafter, there was considerable variability in the ovulation rates. Some 12- or 13-year-old females had particularly high ovulation rates, possibly a result of several initial infertile ovulations (Harrison et al. 1972). Others of the same age had low corpora counts, were all lactating, and one was pregnant, indicating that fertilization occurred on the first or second ovulation. Indirect evidence, which shows that lactational transfer of organochlorines in female bottlenose dolphins occurred after one or two ovulations (Cockcroft et al. 1989), supports the view that the majority of females conceive after one or two ovulations. The variation in ovulation rates of older females may be due, in part, to the same factors which apply to younger females and to additional reasons such as calf mortality or aborted pregnancies.

Overall, the calculated annual ovulation rate for female bottlenose dolphins was 0.28, a substantially lower rate than that observed for *Tursiops* from northeast Florida (Sergeant et al. 1973). There was little sign of reproductive senescence in females from Natal, as ovulation rate did not appear to decline with age, and there was no reduction in ovary mass with an increasing number of ovarian scars. Also, the oldest captured female was lactating, and a number of older females were captured with calves and had enlarged *corpora* in their ovaries. Results from organochlorine residue studies in these females also indicate that older females do not become senescent (Cockcroft et al. 1989). These data imply that older females do not act as "wet nurses," which is contrary to suggestions for several other species of odontocetes that manifest age-related declines in fecundity. Senescent females invest more in quality calf-rearing and a longer lactational commitment than in quantity calf-bearing, as their reproductive potential fails (Kasuya and Marsh 1984, Marsh and Kasuya 1986). However, sample numbers in this study were small and certain female-calf pairs showed an extended relationship, though there was no indication that this was restricted to older females.

Taken in combination, these facts indicate that some Indian Ocean bottlenose dolphin females are probably reproductively active until an advanced age. A similar conclusion was reached by Kasuya (*in* Marsh and Kasuya 1986) who found that although the annual pregnancy rate and the number of resting females in a sample of *Tursiops* from the Pacific declined with age, pregnant and lactating females were present in all age groups, presenting no conclusive evidence of senescence.

Although births apparently occur throughout the year, there is a peak in summer, between November and February, when over 60% of births occur. However, as birth dates were back-calculated, this may reflect the greater catch of dolphins in these months and the bias of the net catch for larger calves (Cockcroft and Ross In press), although previous work in this region noted that births occurred predominantly in late spring and summer (Ross 1977). No seasonal cycle of either testis mass, tubule diameter, or occurrence of sperm in epididymis was evident in mature males. These data also imply no distinct mating or breeding season in Indian Ocean *Tursiops*. In Florida waters, the main mating and calving season is apparently February to May (Essapian 1963), or spring to early fall (Irvine et al. 1981), which is similar to that found in the present study. In contrast, bottlenose dolphins off Argentina show a distinct summer calving and mating season (Wursig 1978). These geographical variations, however slight, indicate the adaptability of coastal *Tursiops* to local conditions.

Although it has been suggested that suckling as a nutritional source probably only lasts 1 year (Kasuya and Marsh 1984, Cockcroft and Ross 1990b), there is evidence that suckling may last at least 18 months in *Tursiops* and that non-nutritional suckling may continue for as long as 3 years for some mother and calf pairs. An estimate of the duration of lactation is difficult, where suckling extends over long periods and may serve a non-nutritional purpose such as enhancing the cow-calf bond (Brodie 1969). Of the calves from lactating female-calf pairs, 25% were over 1 year old and a further 25% were over 2 years old, and some of the latter had both milk and solids in their stomachs. The mammary glands from these lactating females, only one of which was pregnant, increased in size with calf size, until calves were at least 18 months old. In combination, these data indicate that lactation in Indian Ocean bottlenose dolphins lasts more than 1 year and in some instances may extend to more than 2 years.

This is slightly longer than previous estimates of lactation length and age at weaning based on studies of captive and captured free-ranging bottlenose dolphins (McBride and Kritzler 1951, Gurevich 1977, Saayman and Tayler 1977, Kasuya 1985, Cockcroft and Ross 1990b) and suggests a prolonged mother-calf association that may extend in free-ranging bottlenose dolphins for at least 15 months (Irvine et al. 1981). Such extended mother-calf interaction may indicate a stable school structure, such as that postulated for short-finned pilot whales off the Pacific coast of Japan, which may be indicative of late maturing, long-lived animals (Kasuya and Marsh 1984). This may equally apply to *Tursiops* where a lengthy mother-calf bond may be important in the calf's development and be a reflection of the smaller school size and inshore habitat, mastery of which may require greater maternal care and a longer learning period (Cockcroft and Ross 1990b).

During a study of captive bottlenose dolphin mother and calf association, Cockcroft and Ross (1990b) have shown that the calf's suckling rate decreased with age, although its energy requirements probably grow with its level of independence and activity. As there was no evidence of energy changes in delphinid milk during lactation (Arvy 1974) to compensate for this, the authors proposed that the quantity of milk ingested may increase as the calf's stomach volume increased (Cockcroft and Ross 1990b). This explanation is supported by the present findings that a female's mammary glands increase in size, probably increasing the volume of milk produced, during lactation.

In view of the extended lactation period of female bottlenose dolphins and the early and probably increasing intake of solid food by the calf, it is unlikely that females require a substantial interval between the end of lactation and the next pregnancy. A 1-year resting period, estimated from the catch statistics data, is almost certainly an overestimate due to catch bias. Kasuya (1985) estimated a 3-month resting period for *Tursiops* in the western north Pacific, and it is probable that Indian Ocean *Tursiops* are similar. Considering that gestation lasts about 1 year and that lactation probably lasts 18 months to 2 years, a calving interval of around 3 years can be estimated for Indian Ocean bottlenose dolphins. This estimate is in good agreement with the projected ovulation rate of one every 3 years, but assumes that all calves survive and ignores the effects of differential calf mortality (Perrin and Reilly 1984) that would lower the mean calving interval considerably.

Nothing is known of the age and sex structure of the Natal bottlenose dolphin population. The only available information is from the catch of these animals in the Natal shark nets, the sex, size, and age structure bias of which have been discussed (Cockcroft and Ross In press). Given these biases, attempts to calculate reproductive parameters from these data are flawed but provide the only means of calculating the reproductive potential of this population.

The relevant proportions in the net catch of females—mature, lactating, pregnant, and resting—are 56%, 43%, 27%, 5.2%, and 5.8%, respectively (Cockcroft and Ross In press). Annual pregnancy rates (APR; Perrin and Reilly 1984) calculated from these catch data and lactation period (either 1 or 2 years) range between 5.2% and 27%. Changes in either the proportion of females lactating or the length of lactation greatly influence this calculation, but even the highest estimate is low in comparison with values calculated for *Tursiops* in other areas; 63% in the Black Sea (Danilevsky and

Tyutyunnikov 1968, *in* Perrin and Reilly 1984) and 43.6% and 40.4% for the western north Pacific (Kasuya and Izumisawa 1981, *in* Perrin and Reilly 1984; Kasuya 1985).

Gross annual reproduction rate (GARR) (Perrin and Reilly 1984) calculated from catch statistics and the range of APR values yields estimates between 0.043 and 0.065. Although biases in the catch will influence these GARR estimates, they are useful for comparative purposes. The former GARR estimate is greater than that calculated for an unexploited stock of *Tursiops* from eastern Australian waters, although this was based on an unreliable technique of estimating calf numbers from aerial surveys (Lear and Bryden 1980, *in* Perrin and Reilly 1984). The latter GARR figure, although probably an overestimate, is some 40% and 500% lower than those estimated for exploited populations of *Tursiops* off Iki Island, Japan (Kasuya 1985) and in the Black Sea (Danilevsky and Tyutyunnikov 1968, *in* Perrin and Reilly 1984), respectively.

The probable biases in the calculated APR and GARR estimates suggest that an assessment of the theoretical maximum natural rate of increase (ROI) of the Natal bottlenose dolphin population would be more practical. Assuming a calving interval of 2–3 years, age at first breeding of 10 years, and an annual survival rate of less than 0.97, an ROI of 4–6% can be calculated (Reilly and Barlow 1986). The ROI makes allowances for adult and calf mortality not accounted for by a GARR estimate, which, therefore, infers that even the greater GARR figure may be an underestimate. Given an annual increase of as much as 6% of the estimated 900 population, the mean annual mortality of bottlenose dolphins in shark nets—32 dolphins per year including about 4 reproductive females—in conjunction with whatever other sources of man-induced mortality, such as the probable death of first-born neonates through pollutant toxicity (Cockcroft et al. 1989), implies that mortalities may be close to or exceed the likely replacement rate of this population. However, this conclusion should be viewed with some caution, as it is based on an estimated population of only some 900 dolphins, although biases of aerial counts suggest that numbers may be greater (Cockcroft et al. In press). Additionally, other factors may also influence understanding of the reproductive capacity of this population. If bottlenose dolphins on the Natal coast are geographically separated for long periods (Cockcroft et al. 1989) with little mixing even of adjacent groups (Cockcroft et al. In press), then reproductive parameters for females in different areas may vary and have a profound effect on calculated replacement potentials.

The incidental mortality and probable depletion of long-lived dolphins, that invest many years in the care and socialization of their young and are resident in areas with which they are familiar, is of concern. The future management of the Natal bottlenose dolphin population requires accurate population figures and an unbiased estimate of age and sex structure. Regular aerial, boat, and shore-based surveys along the Natal coast are needed to define the former. The latter is best obtained through a combination of intensive field observational work on free-ranging dolphins and a continued monitoring of captured animals.

Acknowledgments

We gratefully acknowledge Shantal Koch and Sabine Klages for many hours spent in preparing histological slides, counting dentine layers, and sectioning ovaries. We appreciate the help of Dr. T. Kasuya for reading a selection of teeth so that we could calibrate our own techniques. Our thanks to the Director and staff of the Natal Sharks Board for their cooperation in collecting animals from the nets.

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Oceanic Dispersion of Larval Fish and its Implication for Mortality Estimates: Case Study of Walleye Pollock Larvae in Shelikof Strait, Alaska

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Abstract.—To estimate mortality and abundance of walleye pollock *Theragra chalcogramma* larvae in Shelikof Strait, Alaska, during spring 1981, a diffusion-advection model, combined with growth and death of fish larvae, was applied. Physical parameters (diffusion coefficients and advection rates) were derived from the distributional variances and centroids of fish larvae collected in ichthyoplankton surveys. The diffusion coefficient and the advection rate in the along-strait direction were 65.2 km^2/day and 2.7–4.2 km/day, respectively, which compared favorably with values obtained from moored current-meter data. Simulation revealed that the expected distribution of larvae was similar to that observed from ichthyoplankton samplings, and that around 20% of the larvae drifted out of the survey area in Shelikof Strait within the 1-month sampling period. The larval fraction dispersed out of the survey area was used to revise larval mortality and abundance estimates. Revised mortality (0.070/day) was close to that (0.063/day) determined from examining larval patches. The simulation in this paper resulted in an increase by a factor of 1.5 in the estimated total larval abundance compared with earlier estimates and field observations.

Manuscript accepted 24 January 1990.
Fishery Bulletin, U.S. 88:303–311.

Most marine fish have a period of planktonic existence during egg and larval stages. Since early in this century it has been believed that survival during early life determines year-class strength and recruitment variability to fisheries (Hjort 1914). Furthermore, recruitment processes are quite complex because the biological and environmental factors which act on eggs and larvae are closely related (Wooster et al. 1983). Hence, the relationship between organisms and their environment is critical for understanding recruitment variability. The observed patterns of egg and larval distributions can be considered to be the result of a combination of fundamental processes, including spawning time and location, advection, diffusion, growth and mortality. These parameters could be identified using biological data.

The early-life stages of walleye pollock *Theragra chalcogramma* whose biomass is the largest of a single species in world fisheries (Sharp 1987), have been the objects of considerable research in recent years. In Shelikof Strait (Fig. 1), about 90% of the eggs were produced between 25 March and 15 April 1981, and they have approximately a 2-week embryonic period at 5°C (Kim 1989). Spawning produces a patch of planktonic eggs and larvae that can be followed as they develop and are advected in prevailing currents toward the southwest. In Shelikof Strait walleye pollock eggs exist at depths below 150 m due to their high specific gravity. Their transport rate from the spawning area is very small because of weak circulation in deep water (Kendall and Kim 1989).

Eggs of late developmental stage would move upward fast due to the decreased specific gravity of old eggs, and the eggs hatch mid-depth in the water column (Kim 1987). Also the specific gravity of newly hatched larvae is continuously decreasing, so that most larvae are found within the upper 60 m of the surface (Kendall et al. 1987). Kim and Kendall (1989) described the distribution and transport pattern of larvae in Shelikof Strait during spring. Young larvae occupy a relatively small area and form a dense patch, while older larvae spread over a broader area in Shelikof Strait, showing the importance of diffusion on the larval patch. These larval patches have been identified for at

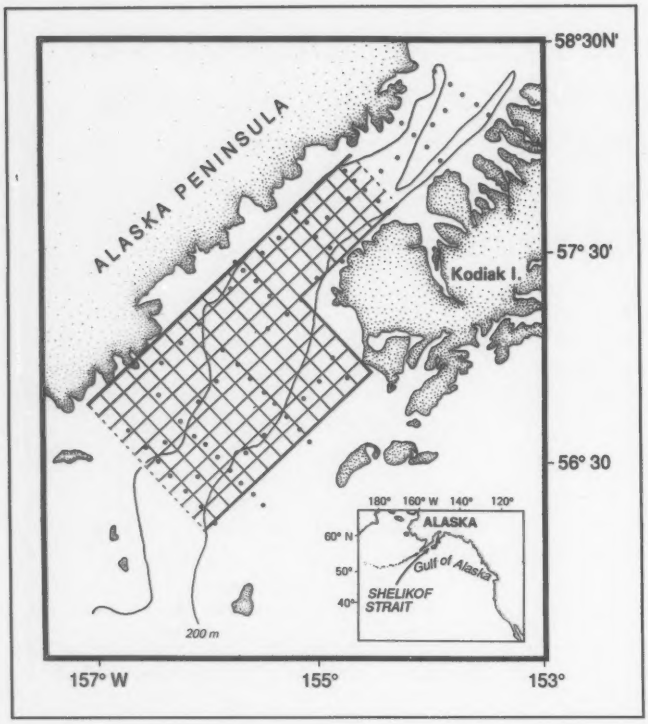

Figure 1
Typical locations of sampling stations (•) and the grid pattern used for the computer simulation. The flux of larvae through the solid lines is zero. The dashed lines are open boundaries of the model that permit the loss of larvae.

least a month after hatching (Incze et al. 1989). Assuming no drift or dispersion of larvae away from the sampling area, the instantaneous daily mortality was estimated as 0.086 (Kim and Gunderson 1989). The effects of advection and diffusion on the larval mass, however, can cause errors in estimation of mortality and abundance. Hence, the distribution and abundance of walleye pollock larvae in Shelikof Strait should be reconsidered in the light of oceanic diffusion-advection theory (McGurk 1989).

The main objectives of this paper are:

1 Estimation of diffusion coefficients and advection rates of walleye pollock larvae based on ichthyoplankton distribution in Shelikof Strait;

2 Description of expected larval distribution and abundance with time from a computer simulation using a diffusion-advection model; and

3 Reestimation of larval mortality and expected larval abundance reported in Kim and Gunderson (1989) and comparison of these results with field observations.

Background of theories and model

In general, the simplest approach to the diffusion problem for particles in a fluid medium follows from the assumption that the rate of diffusion is directly proportional to the local concentration gradient (Okubo 1980). Walleye pollock larvae in Shelikof Strait are advected and diffused in the upper 60 m during early larval stages (Kendall et al. 1987), and the swimming ability of larvae less than 10 mm is assumed to be inconsequential. Therefore, a horizontal two-dimensional diffusion-advection model is applicable to changes in the distribution and abundance of young walleye pollock larvae in Shelikof Strait. Current speeds (u and v) and diffusion coefficients (K_x and K_y) are set constant, with the assumption of a homogeneous turbulence field and negligible horizontal divergence. Newly hatched larvae (i.e., the source material in the diffusion-advection model) are assumed to be produced daily at a fixed location near the center of Shelikof Strait (Kim and Kendall 1989). Once larvae that dispersed from the source point arrived at the Alaska Peninsula coast, they were required to remain there, since the shallow coastal region is considered a nursery area of young fish (Walters et al. 1985). Since larvae grow as they drift, the simulated distribution and abundance of larvae can be divided into several size groups. The partial differential equation, with initial condition $C_i(x,y,T_1) = 0$ and boundary conditions as described above, is

$$\frac{\partial C_i}{\partial t} = K_x \frac{\partial^2 C_i}{\partial x^2} + K_y \frac{\partial^2 C_i}{\partial y^2} - u \frac{\partial C_i}{\partial x} - v \frac{\partial C_i}{\partial y} - rC_i \quad (1)$$

where C_i = larval concentration of i-th cohort (number/m^2),
x and y = along- and cross-strait coordinates,
K_x and K_y = along- and cross-strait turbulence diffusion coefficients,
u and v = along- and cross-strait velocity components,
r = instantaneous daily mortality of larvae, and
T_1 = starting time of i-th cohort larval production.

The solution using Laplace transform is

$$C_i(x,y,t) = \frac{1}{4\pi\sqrt{K_x K_y}} \int_{T_1}^{t} \frac{P_i(T)}{(t-T)} e^{r(t-T)} \left\{\sum_a e^{-\frac{(x-A_a)^2}{4K_x(t-T)}}\right\}\left\{\sum_b e^{-\frac{(y-B_b)^2}{4K_y(t-T)}}\right\} dT \quad (2)$$

where $C_i(x,y,t)$ = larval concentration of i-th cohort at time t at point (x,y),
$P_i(T)$ = i-th cohort's larval production rate at time T ($T_1 < T < t$) and at source point (x_0, y_0).

$$A_a = (-1)^{|a|} X^* + a(x_{+L} - x_{-L}) + \mathrm{mod}(|a|,2)(x_{+L} + x_{-L})$$

$$B_b = (-1)^{|b|} Y^* + b(y_{+L} - y_{-L}) + \mathrm{mod}(|b|,2)(y_{+L} + y_{-L})$$

where a and b = indices of symbol summation (Σ)
if there is no boundary, a or $b = 0$
if there is negative-side ($-L$) boundary only, $a = -1, 0$; $b = -1, 0$
if there is positive-side ($+L$) boundary only, $a = 0, 1$; $b = 0, 1$,
if there are boundaries at both sides, $a = -\infty, \ldots, 0, \ldots, +\infty$, $b = -\infty, \ldots, 0, \ldots, +\infty$

$X^* = x_0 + u(t-T)$
$Y^* = y_0 + v(t-T)$

x_{+L}, x_{-L}, y_{+L}, and y_{-L} = positive and negative side boundaries in x and y coordinates,
mod($|a|$,2) = remainder of $|a|$ divided by 2, and
mod($|b|$,2) = remainder of $|b|$ divided by 2.

The area of Shelikof Strait used in the computer simulation was divided into 162 10×10 km grid areas with boundaries along the Alaska Peninsula and Kodiak Island (Fig. 1). The grid scheme was used to obtain contour patterns of results and to compare the simulated values with observations. To obtain larval abundance for each grid area from Equation (2), numerical integration was used, since the integration could not be handled by further analytic approach. For time integration, an 8-point Gaussian Quadrature is used (Scheid 1968), and for spatial integration an error-function infinite series is used (Gradshteyn and Ryzhik 1980).

Once all parameters were selected for the diffusion-advection equation, the simulation program was run for 50 days starting on 5 April (Julian day 95) and continuing until 24 May (Julian day 144). Larvae were produced near the central strait every day. They then were advected and diffused in the grid area according to given values of the parameters. Finally the concentration obtained from the model for each size group during the 5-day period of 20–24 May was averaged to show the expected larval abundance of each size group in late May 1981.

The mortality parameter in Equations (1) and (2) was derived in Kim and Gunderson (1989) from observed data during two consecutive surveys (i.e., 26–30 April and 20–24 May, 1981) assuming that larvae stayed in the survey area and that the larval population decreased exponentially with time. If, however, some of the larval cohort that existed in the sampling area during the first survey drifted out of the area by the second survey (called out-fraction in this paper), then the mortality rate must be an overestimate. The out-fraction of larval abundance—which is the ratio of the larval abundance evicted from the simulation box in Figure 1 to the total larval abundance assuming no dispersion—is computed after simulation, and this computation can be used to estimate a new mortality value in an exponentially decreasing population with time:

$$Z^*(L) = -\frac{1}{\Delta T} \ln\left\{\frac{d_2/(1-f)}{d_1}\right\} = -\frac{1}{\Delta T} \ln\left\{\frac{d_2}{d_1}\right\} + \frac{1}{\Delta T} \ln(1-f) \quad (3)$$

where $Z^*(L)$ = revised instantaneous daily larval mortality,
ΔT = time difference in days (24 days) between surveys,

d_1 and d_2 = observed larval densities during late April and late May surveys, respectively, and
f = out-fraction.

Note that the first term of the right side means the daily mortality rate for the closed population, which was used in Kim and Gunderson (1989), and that the second term is the correction factor due to dispersion. Once the new mortality rate was determined, it was used for the second simulation to obtain a revised estimate of larval abundance in late May 1981.

Parameter estimation

Some parameters for the model were available from other studies. Kim and Gunderson (1989) found two dominant larval cohorts during April and May surveys, and assumed that 4–5 mm larvae in late April had grown to 8–9 mm, and regarded this group as cohort 1. Also, the 5–6 mm size class in late April and the 9–10 mm size class in late May were treated as cohort 2. By comparing the larval abundances of these two cohorts, they estimated an instantaneous daily larval mortality of 0.086 and a daily growth rate of 0.17 mm.

Daily larval production was derived from daily egg production and time-specific egg mortality during development (Kim and Gunderson 1989). A rapid increase in daily larval production occurred in mid-April, and most larvae were produced during late April (Table 1). Toward the end of the spawning season, larval production decreased but tended to be prolonged due to decreased egg mortality late in the spawning season.

Advective velocities and turbulent diffusivities were derived by examining changes in the distributional centroids and variances of several larval size groups. We treated the distribution of a certain size of larvae at a specific time as a single dispersing system in Shelikof Strait. The change in the centroids in along- and cross-strait coordinates for three size groups (4–5, 5–6, and 6–7 mm) from each survey was used to estimate advection, assumming that larvae were hatched in the same area and that these larvae were not flushed out of

Table 1
Estimates of daily larval production of walleye pollock after 14-day incubation period in Shelikof Strait during spring 1981, using estimated daily egg production and time-specific egg mortality in Kim and Gunderson (1989). Dates 95 and 144 denote 5 April and 24 May, respectively.

Date of year	Daily larval production ($\times 10^9$)	Date of year	Daily larval production ($\times 10^9$)
95	23	120	1103
96	48	121	1027
97	77	122	938
98	111	123	835
99	151	124	717
100	197	125	584
101	250	126	435
102	311	127	270
103	380	128	37
104	458	129	38
105	546	130	37
106	1016	131	38
107	1557	132	38
108	2174	133	39
109	2873	134	39
110	3087	135	38
111	3311	136	38
112	3545	137	38
113	3790	138	37
114	3294	139	37
115	2711	140	36
116	2034	141	35
117	1257	142	34
118	1217	143	33
119	1166	144	32

Table 2
Comparison of walleye pollock larval mortality rates, advection rates, and diffusion coefficients in Shelikof Strait during spring 1981.

	Instantaneous daily mortality	Advection rate (km/day)				Diffusion coefficients (km²/day)	
		u		v			
		April	May	April	May	K_x	K_y
This paper	0.070	4.2	2.7	1.3	0.4	65.2	3.6
Reed et al. (1989)	0.063	4.3		—		43.2	—

Shelikof Strait. Estimates of u and v, from regression analysis (see Table 1 in Kim and Kendall (1988) for data) were 4.2 and 1.3 km/day in April, and 2.7 and 0.4 km/day in May, respectively (Table 2). Because the variance of the horizontal distribution is a suitable measure of the spread of the substance (Bowden 1983, Okubo 1971), the change in variance (i.e., S_x^2 and S_y^2 for along- and cross-strait directions) with time provides a reasonable measure of the diffusion coefficient;

$$K_x = \frac{1}{2}\frac{dS_x^2}{dt} \cong \frac{S_{x,t1}^2 - S_{x,t0}^2}{2\Delta t} \quad (4)$$

$$K_y = \frac{1}{2}\frac{dS_y^2}{dt} \cong \frac{S_{y,t1}^2 - S_{y,t0}^2}{2\Delta t} \quad (5)$$

where $S_{x,t0}^2$, $S_{x,t1}^2$, $S_{y,t0}^2$, and $S_{y,t1}^2$ are the spatial variances at time $t0$ and time $t1$ in along- and cross-strait directions, and $\Delta t = t1 - t0$. The variances of two dominant larval cohorts were calculated as in Kim (1987). Variances of larval distribution were much increased in a month, and along-strait components were dominant compared with those in the cross-strait direction (Table 3). The estimated K_x for these two cohorts were 79.6 and 50.7 km^2/day (average 65.2). For K_y, the values were 1.0 and 6.3 km^2/day (average 3.6) (Table 2).

Table 3
Spatial variances of larval distributions of two major cohorts of walleye pollock larvae in Shelikof Strait during late April and late May 1981. The larval sizes of cohorts 1 and 2 in late April are 4–5 mm and 5–6 mm, and they grow to 8–9 mm and 9–10 mm in late May, respectively.

		Variance (km^2)	
		late April	late May
Cohort 1	S_x^2	1292	5114
	S_y^2	563	609
Cohort 2	S_x^2	3066	5500
	S_y^2	302	606

Simulation results

Spatial distribution and abundance of larvae

The model distribution of larvae in late May after 50 days of simulation was similar to that observed. Two major larval cohorts, 8–9 mm and 9–10 mm size groups, were selected for comparing the model and observed distributions (Fig. 2). In general, the simulated centroids of distribution were close to the densest patches of the larvae, and the area of larval distribution and contour levels of the larval concentrations were not very different from those observed. The simulation demonstrated the elliptical pattern of distribution, which was elongated in the along-strait direction, and the southwesterly movement of centroids from the main hatching area. The first (8–9 mm) and second (9–10 mm) cohorts drifted 92 km and 114 km, respectively, from the source point after hatching.

The maximum size of larvae was 12 mm, and the abundance of larvae and the out-fraction in each size group were computed. Comparing the simulated values with the observed ones, we found that the results were very close (Table 4). Also, as expected, the effect of out-fraction on larval distribution was more important for the larger size group than the smaller group. This was caused by the larger larval size having a higher out-fraction value. Negligible amounts of small larvae were advected from the simulation box, but over 50% of the large larvae were removed. Among total larval abundance, about 20% were flushed out of the simulation area. This concept of out-fraction due to diffusion and advection might change the larval abundance and mortality previously reported by Kim and Gunderson (1989). Even though their derived estimates agreed well with observed ones, their results should be reconsidered because the areas involved for abundance estimates were not the same. Our study revealed that their sampling area, which was similar to our simulation box, was only part of the area of larval occurrence in Shelikof Strait. Therefore the total larval abundance should be higher than they observed, and the simulated abundance within the simulation box should be close to that observed. In Table 4, the reason for the smaller larval abundance in the simulation box (3.37×10^{12}) than observed (4.15×10^{12}) might be due to their overestimate of the mortality rate.

Re-estimation of larval mortality and abundance

The first approximation of larval mortality has been recalculated using the out-fraction in Table 4. By applying the out-fractions of the two major cohorts to Equation (3), we computed revised instantaneous daily mortalities of 0.081 and 0.059 from the first and second cohorts, respectively (average 0.070). Assuming no significant change in diffusion coefficients, the revised mortality rate was used for the second computer simulation of the diffusion-advection model. Figure 3 revealed that the second simulation resulted in a 50% increase in the total larval abundance (6.21×10^{12}) in Shelikof Strait, compared with the first simulation (4.23×10^{12} from Table 4). The size-specific abundance

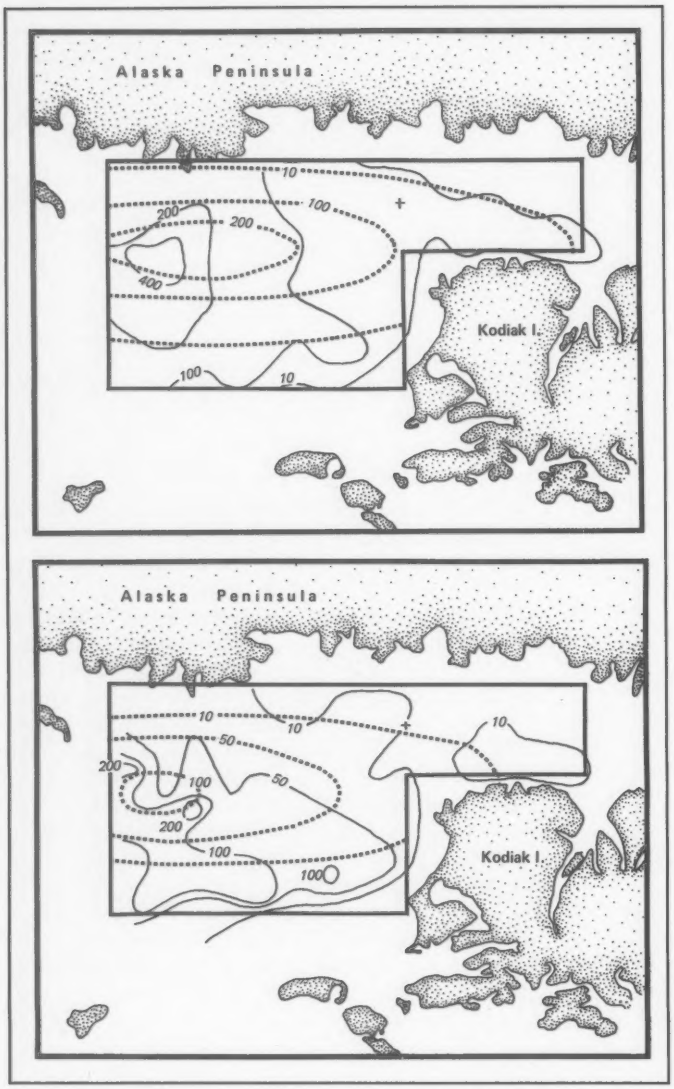

Figure 2
Contours of observed (———) and estimated (---) distributions of (a) 8–9 mm and (b) 9–10 mm walleye pollock larvae during late May 1981. Source points of larvae are indicated by (+) in each map.

of larvae within the simulation box was compared with the observed values, because the area used in the simulation could be regarded as the survey area. In general, the trends in size abundance curves, as well as the absolute abundances, were very similar to one another. The abundance of two major cohorts, both observed and simulated, consisted of about 50% of the total abundance.

Discussion

The application of a diffusion-advection model to examine the dispersal of larvae helps not only to explain spatiotemporal distribution of abundance but also to revise estimates of population parameters such as larval mortality. Difficulties in determining parameter values, however, often arise in this kind of study. In describing plankton distribution, the physical properties (diffusion coefficients and advection rates) often

Table 4

Simulated abundances of walleye pollock larvae in Shelikof Strait during late May 1981 resulted from the first computer simulation, using a daily instantaneous mortality rate of 0.086 and observed values derived from Kim (1987).

Larval size (mm)	Simulated larval abundance ($\times 10^{12}$)		Out-fraction	Observed larval abundance ($\times 10^{12}$)
	Total	Simulation box		
<4	0.033	0.033	0.0000	0.004
4–5	0.157	0.157	0.0006	0.057
5–6	0.112	0.111	0.0128	0.111
6–7	0.627	0.593	0.0538	0.496
7–8	1.011	0.881	0.1281	1.221
8–9	1.509	1.120	0.2576	1.350
9–10	0.701	0.436	0.3786	0.627
10–11	0.073	0.035	0.5200	0.204
11–12	0.008	0.003	0.6367	0.058
Total	4.230	3.369	0.2036	4.149

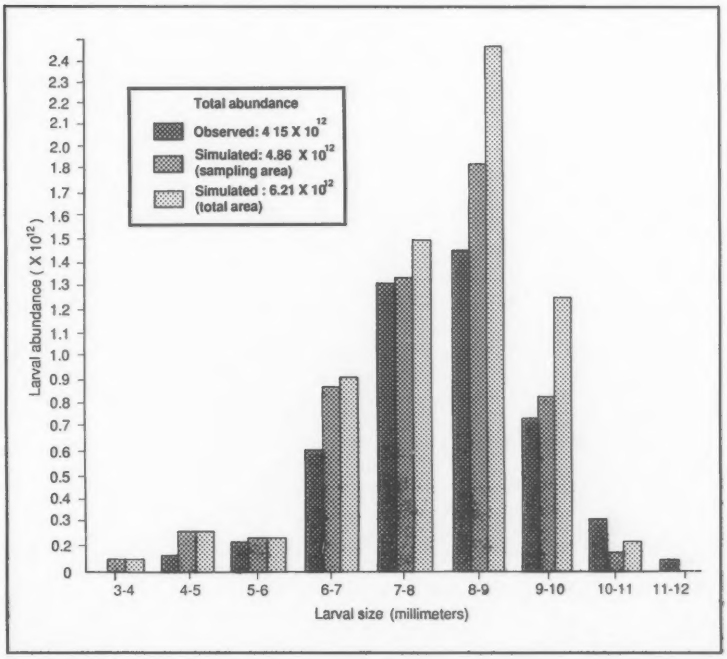

Figure 3

Simulated larval abundance from the second computer simulation using a revised mortality rate of 0.070/day, and observed larval abundance in Table 3. Notice the difference in the simulated abundances from the sampling area and the total area.

are calculated from oceanic current data, wind speed, temperature distribution, or results of dye experiments (Talbot 1974, Talbot 1977, Power and McCleave 1983, Sundby 1983), even though they do not represent the actual diffusion and advection of dispersing organisms. The collection of diffusion coefficients and advection rates from several sources is very important to understand the characteristics of the oceanic situation. Aside from measuring the dispersion using inert tracers, the use of plankton sampling data to derive these parameters has been limited because of the complexity of biological systems in the sea. The mobility and mortality of larvae may bias in estimating such parameters. The emphasis of this paper is how biological sampling data can be used for estimating physical properties, when the swimming ability of the larvae is not significant.

Reed et al. (1989) estimated parameters based on current measurement and larval patch in Shelikof Strait. By examining the abundance in small areas around the densest larval patches found in April and May surveys, they estimated an instantaneous mortality rate of 0.063/day and an advection rate of 4.3 km/day (Table 2), which are in excellent agreement with our estimates. Also, the estimation of eddy diffusivity in the along-strait direction of 43.2 km^2/day by Reed et al. (1989) did not differ greatly from our mean value of 65.2 km^2 (Table 2), even though the former was derived from moored current meter data in the surface layer (56 m) and the latter from larval distribution. These estimates are realistic only in a mean sense, because they vary in both time and space.

The diffusion process tends to destroy larval aggregation until larvae reach a certain size, so that patchiness will decrease with time. The Lloyd Patchiness Index (LPI) has been frequently used for describing aggregations of organisms (Lloyd 1967), and Kim (1987) discussed changes in LPI of walleye pollock larvae as they grew. The smaller size groups of larvae usually had a higher LPI, but it decreased until a size of about 10 mm because of dispersal of the larval patch. For sizes greater than 10 mm, although their contribution to the total larval abundance was very small, the LPI increased with length, perhaps because of reaggregation of the larvae as their swimming ability increased. If a larval retention mechanism worked for large larvae (10–12 mm) in Shelikof Strait due to increased swimming ability, that might explain the higher larval abundance from field samplings than that from the simulation shown in Figure 3. Similar examples of larval aggregation (i.e., initially patchy, dispersing until a larval size of around 10 mm, and then patchy again) were reported for northern anchovy and jack mackerel off California (Hewitt 1982).

The expected total larval abundance from the first simulation was almost identical to that in Kim and Gunderson (1989) because the same parameter values were used. By adding the concept of diffusion and advection to their model, elaborations on mortality and expected abundance of walleye pollock larvae were made. Based upon good agreement between observed and simulated results, this paper has emphasized that dispersion (or emigration) of organisms is important in the field of population dynamics.

Acknowledgments

We are indebted to many people for helping us complete this manuscript. We would like to thank P. Stabeno, R. Reed, and J. Schumacher at the NOAA Pacific Marine Environmental Laboratory and A. Okubo at State University of New York at Stony Brook for their comments and advice. Also we are greatful to all FOCI (Fisheries Oceanography Coordinated Investigation) members of AFSC (Alaska Fisheries Science Center) who have prepared and provided us the necessary data. Special thanks is given to A. Kendall (AFSC) who funded this project and gave us valuable comments.

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Tag Shedding by Southern Bluefin Tuna *Thunnus maccoyii*

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Abstract.—Models are formulated for estimating tag-shedding rates from recapture records for eight double-tagging experiments with southern bluefin tuna (*Thunnus maccoyii*) in three Australian fishing areas. These models incorporate either a constant or time-varying rate of tag shedding and allow for the possibility of immediate tag shedding. Likelihood ratio tests are used to select the most parsimonious model for each data set. The probability of a tag being shed after 4 years at liberty (the length of the most recent experiments) varied from around 0.2 for the 1983 and 1984 experiments to 0.5–0.7 for the experiments carried out in the 1960s and 1970s. Although a single, best-fitting model was selected in all but one experiment and despite the large total numbers of recoveries, precise estimates of long-term shedding rates could not be obtained because there were relatively few long-term data. This has significant implications for analyses of tag-return data that give heavy weighting to long-term recaptures.

Manuscript accepted 11 December 1989.
Fishery Bulletin, U.S. 88:313–321.

Southern bluefin tuna *Thunnus maccoyii* were tagged throughout the 1960s in three areas of major Australian commercial fishing activity: off the south coast of Western Australia (WA), in the Great Australian Bight off South Australia (SA), and off the south coast of New South Wales (NSW). During the 1970s, tagging took place mainly off WA. The aim of these experiments was to provide information on movements, growth, and mortality of the southern bluefin. In 1983 and 1984, new experiments were initiated off WA and SA in order to answer more specific questions relating to fishery interactions, yield-per-recruit, and schooling behavior, as well as to update information obtained from the previous experiments (Majkowski and Murphy 1983). Apart from the period prior to 1963, almost all fish were double tagged.

Quantitative analyses of tagging data that require an estimate of the total number of recaptures of tagged fish (e.g., fishery interactions, yield-per-recruit, and mortality) need to take account of tag loss due to shedding. As reviewed by Wetherall (1982), this problem can be approached in two ways. If estimation of mortality rates is the main objective of the analysis, one can attempt to model the entire process of removal of tags from the population directly by incorporating into the model parameters that account for all sources of removal, i.e., natural mortality, fishing mortality, permanent emigration, nonreporting of recaptured tags, and tag shedding. Alternatively, tag-shedding rates may be estimated independently from a double-tagging experiment and the recovery data adjusted accordingly before proceeding with further analyses (other losses, e.g., non-reporting, may also require independent estimation). A disadvantage of the former approach is that, even if simple functions are chosen to describe mortality, emigration, and tag shedding, the model will inevitably be parameter-laden, and therefore difficult to estimate. In any case, such models will not necessarily lend themselves to analyses of interactions and yields-per-recruit, where the mortality and emigration processes are embedded in the recapture statistics and do not necessarily require explicit resolution (Majkowski et al. 1984).

The aim of this paper is to estimate tag-shedding rates for a number of southern bluefin tuna double-tagging experiments, with a view to using these estimates as the basis for correcting for tag shedding in other analyses. Hynd (1969) made a preliminary estimate of the tag-shedding rate, assumed constant, based on recoveries up to 1968 only. Subsequently, Kirkwood (1981) developed generalized tag-shedding models and analyzed recoveries of southern bluefin tuna that were double tagged during the period 1962–76 but excluded all tagging that was contracted to fishermen. In both cases, these analyses used tag-recovery data that were grouped by time of recovery. A reevaluation of southern bluefin tuna tag shedding is now appropriate because, (1) for a number of present

Table 1

Double-tagging experiments of southern bluefin tuna in the New South Wales (NSW), South Australia (SA), and Western Australia (WA) areas.

Experiment number	Area	Years	Carried out by	Fishing method	Tagging method	Number released	Number[1] recovered with 2 tags	Number[1] recovered with 1 tag
1	NSW	1963–70	CSIRO	Pole	Board[2]	2770	253	153
2	NSW	1963–70	Fishermen under contract to CSIRO	Troll	Board	9513	3199	862
3	SA	1964–69	CSIRO	Pole	Board	7328	929	300
4	SA	1977	CSIRO	Pole	Board	908	164	54
5	WA	1963–67	CSIRO	Pole	Board	12826	264	264
6	WA	1970–78	WA Dep. Fisheries	Pole	Board	5692	236	120
7	WA	1983	CSIRO	Pole	Cradle[3]	6907	1853	472
8	SA	1984	CSIRO	Pole	Cradle	3211	1117	176

[1]Excludes recoveries for which an accurate recapture date was not available.
[2]Fish placed on a measuring board for tagging.
[3]Fish placed in a specially designed cradle for tagging.

applications, it is necessary that the data be analyzed as a series of separate release sets rather than as a pooled data set, and corresponding shedding-rate estimates are thus required; (2) there are now reliable recovery data for 10,416 double-tagged southern bluefin available for analysis (compared with the 1511 recoveries considered by Kirkwood 1981); and (3) models are now available that utilize exact periods at liberty rather than data aggregated by time period. Provided accurate recapture times are available (as is the case here), these new models are preferable because of their greater ability to deal with low recovery numbers towards the end of an experiment.

Tagging data and tagging methods

The tagging data used in this analysis consist of all records received by 31 March 1987 of southern bluefin that were originally double-tagged and that had accurate recapture dates. Recovery dates were considered accurate if at least the month of recapture was known with certainty. In total, there were 10,416 recoveries that met this criterion. Of these, there were 671 recoveries for which the month of recapture was known but the exact day was uncertain; however in almost all of these cases, the uncertainty was estimated to be no more than ± 5 days.

The data were grouped into eight double-tagging experiments: (1) NSW releases 1963–70 (CSIRO*); (2) NSW releases 1963–70 (fishermen contracted by CSIRO); (3) SA releases 1964–69 (CSIRO); (4) SA releases 1977 (CSIRO); (5) WA releases 1963–67 (CSIRO); (6) WA releases 1970–78 (WA Dep. Fish.); (7) WA 1983 (CSIRO); and (8) SA 1984 (CSIRO). This classification of the data was made to ensure that, within experiments, the geographical area, fish size, tagging and fishing methods, and tagging personnel were as similar as possible.

Except for experiment 2, the primary method used to catch fish for tagging was commercial bait and pole; in experiment 2, trolling was used. In all experiments, fork lengths of the fish selected for tagging were measured before tagging. For the first six experiments, this was done by placing the fish on a measuring board. In experiments 7 and 8, the fish were placed in a specially designed vinyl cradle supported by a metal frame and their fork lengths measured using graduations marked on the cradle. While the fish were restrained on the measuring board or in the cradle, two numbered tuna tags of a standard type (Williams 1982) were inserted forward into the musculature at an angle of about 45°, 1–5 cm below either side of the posterior insertion of the second dorsal fin. Ideally, the tag barb anchored behind the second dorsal fin ray extensions or the neural spines, and in experiments 7 and 8 greater effort was made to achieve this than in earlier experiments.

A summary of the fishing method, tagging method, and the numbers of tuna released and recovered is given for each experiment in Table 1. For ease of presentation, the numbers of recoveries in each experiment are grouped by period at liberty in Table 2; as noted above, exact times at liberty for each recovery were used in the subsequent analyses.

*Tagged by staff of the Commonwealth Scientific and Industrial Research Organization (CSIRO).

Table 2

Numbers of double-tagged southern bluefin tuna, for which accurate recapture dates are known, that were reported to have retained both tags (D) or only one tag (S) on recapture, listed by period at liberty.

Period at liberty (yr)	Experiment number															
	1		2		3		4		5		6		7		8	
	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
0–1	175	61	2638	467	831	158	128	23	166	84	205	73	1428	314	644	64
1–2	70	61	517	329	51	76	30	15	72	108	23	31	306	102	381	75
2–3	6	21	37	52	15	19	3	11	18	27	2	7	101	40	82	35
3–4	1	1	4	5	11	9	2	4	—	8	3	4	18	16	10	2
4–5	1	1	1	1	10	11	—	—	3	15	1	2				
5–6	—	—	—	1	2	10	—	—	3	9	—	2				
6–7	—	2	1	2	2	7	—	—	1	4	2	1				
7–8	—	2	—	1	2	1	—	—	—	—	—	—				
8–9	—	1	—	1	2	6	1	1	—	4	—	—				
9–10	—	1	—	1	2	—	—	—	—	1	—	—				
10–11	—	—	1	1	—	1	—	—	—	—						
11–12	—	—	—	—	1	1			—	1	—	—				
12–13	—	—	—	—	—	—			—	—	—	—				
13–14	—	—	—	—	—	—			—	2	—	—				
14–15	—	2	—	—	—	—			—	—	—	—				
15–16	—	—	—	—	—	—			—	1	—	—				
16–17	—	—	—	1	—	1			—	—	—	—				
17–18	—	—	—	—	—	—			1	—						

Tag-shedding models

Various models have been proposed to describe the process of tag loss (Beverton and Holt 1957 and reviews by Ricker 1975; Wetherall 1982). Tag losses can be classified as type I losses, which effectively reduce the number of tags released (immediate tag shedding, immediate tagging mortality, and non-reporting), and type II losses which occur steadily over time (natural mortality, fishing mortality, permanent emigration, and long-term tag shedding). Considering the shedding process only, the simplest model is that proposed by Beverton and Holt (1957) for type II shedding, where the instantaneous rate of shedding (L) is constant over time. In this model, if for a fish originally single-tagged, $Q(t)$ is the probability of the tag being retained at time t after release, then

$$Q(t) = e^{-Lt} \quad (1)$$

If immediate tag shedding occurs, with a probability $1\text{-}\rho$ of this occurring, then

$$Q(t) = \rho\, e^{-Lt} \quad (2)$$

In some cases, it may be inappropriate to assume a constant shedding rate. Some tags may deteriorate over time, causing their shedding rate to increase (Baglin et al. 1980). Alternatively, some tags may be come more securely fixed over time, e.g., through the gradual laying down of tissue around the tag, causing the shedding rate to decrease (Kirkwood 1981). More generally, Kirkwood (1981) has noted that if individual tags have a different propensity for shedding, then the apparent average shedding rate will decrease with time at liberty, as the tags with the higher shedding rate are lost first. Kirkwood modeled this process by allowing the shedding rate to be a gamma-distributed random variable, rather than a constant; however, his model did not allow for an increasing shedding rate. An alternative approach was adopted by Wetherall (1982), who assumed that the probability of a tag being shed was time-dependent. He proposed a flexible function that allowed either an increasing or decreasing shedding rate.

In this paper, we adopt a time-dependent shedding-rate model that allows the probability of an individual tag being shed to decrease over time in an identical fashion to the average shedding rate of the Kirkwood (1981) model. In this case, we now assume that the rate of shedding at time t after release follows the functional form

$$L(t) = \frac{b\lambda}{b + \lambda t}.$$

It then follows that

$$Q(t) = e^{-\int_0^t L(u)\,du} = \left[\frac{b}{b+\lambda t}\right]^b. \quad (3)$$

Note that as $b \to \infty$, $\left[\frac{b}{b+\lambda t}\right]^b \to e^{-\lambda t}$ and $L \to \lambda$. That is, the variable-rate model reverts to the constant-rate model. If a proportion $1-\rho$ of tags are shed immediately, then

$$Q(t) = \rho\left[\frac{b}{b+\lambda t}\right]^b. \quad (4)$$

Parameter estimation

Because only tag returns with accurate recapture dates are considered, an extension of the maximum likelihood estimation procedure used by Kirkwood and Walker (1984) can be used. Suppose fish are double tagged and all tags not immediately shed have identical shedding probabilities that are independent of their companion tags' status (already shed or still retained). Then, if $p_2(t)$, $p_1(t)$, and $p_0(t)$ are the probabilities of a fish retaining two, one, and zero tags, respectively, at time $t\,(0<t<\infty)$ after release,

$$p_2(t) = Q(t)^2,$$

$$p_1(t) = 2Q(t)\,[1-Q(t)]$$

and

$$p_0(t) = [1-Q(t)]^2.$$

A fish that has shed both tags will not normally be distinguishable from a fish that was never tagged. Consequently, the tag-recapture data consist of recoveries of fish retaining one or more tags. Conditional on retention of at least one tag, the probability of a recaptured fish retaining two tags at time t is

$$\frac{p_2(t)}{1-p_0(t)}$$

and that of a recaptured fish retaining one tag is

$$\frac{p_1(t)}{1-p_0(t)}$$

Following an initial release of double-tagged fish at time $t=0$, suppose m fish bearing two tags were recaptured at times $t_{2i}(i=1,\ldots,m)$, and n bearing one tag were recaptured at times $t_{1j}(j=1,\ldots,n)$. Then, the log-likelihood L of the data, conditional on the recapture times $\{t_{2i}\}$ and $\{t_{1j}\}$, is

$$L = \sum_{i=1}^{m} \ln\left[\frac{p_2(t_{2i})}{1-p_0(t_{2i})}\right] + \sum_{j=1}^{n} \ln\left[\frac{p_1(t_{1j})}{1-p_0(t_{1j})}\right].$$

Estimates of the model parameters incorporated in $p_2(t)$, $p_1(t)$, and $p_0(t)$, and their asymptotic variances, can then be obtained by maximizing L using standard methods (e.g., Bard 1974).

Model selection

For each of the experiments, we attempted to select the most parsimonious model. Accordingly, we first fitted model (4), which incorporates immediate tag shedding and (with $b<\infty$) a time-varying shedding rate. Then likelihood-ratio tests (Kendall and Stuart 1961) were carried out to test the null hypotheses that (1) $\rho=1$ (no immediate tag shedding), (2) $b=\infty$ (constant shedding rate), and (3) both $\rho=1$ and $b=\infty$. Unfortunately, since these hypotheses are not fully nested, some ambiguity can still remain. The choice is clear-cut if none of the three hypotheses is rejected, or if all but one are rejected. However, it is possible that while hypothesis (3) is rejected, neither (1) nor (2) is rejected. In that case, there is no reliable basis to distinguish between models (2) and (3).

Particularly when performing non-linear estimations such as these, it is essential to examine the fit of the estimated model to the observed data. Unfortunately, since we are maximizing a likelihood conditional on the observed recapture times, there is no exact way of doing this. As an approximation, however, we can examine the fit of the estimated models to recovery data grouped by time intervals. From the data in Table 2, it is a simple matter (e.g., based on equation 9 in Wetherall 1982) to calculate, for each k, estimates of the proportions of tags shed (P_k) by time t_k, the midpoint of the k-th time interval since release, as well as exact 95% confidence intervals for these proportions based on the binomial distribution. If it is assumed that all tags shed during the k-th time interval were shed at time t_k, then the fitted model and "observed" proportions can be displayed on the same graph. For the grouped data in Table 2, time intervals of one year were used for the first five periods after release. The relatively few longer-term recoveries were grouped into periods at liberty of 5–10 years and 10–20 years.

Table 3
Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using ungrouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm SE$	$\beta \pm SE$	$\rho \pm SE$
1	2	0.29 ± 0.05	∞	0.93 ± 0.02
	3	1.00 ± 0.33	0.26 ± 0.10	1.0
2	2	0.17 ± 0.01	∞	0.976 ± 0.006
3	3	0.78 ± 0.12	0.26 ± 0.05	1.0
4	2	0.17 ± 0.04	∞	0.96 ± 0.01
5	3	1.04 ± 0.28	0.36 ± 0.11	1.0
6	2	0.19 ± 0.05	∞	0.90 ± 0.02
7	3	5.08 ± 2.02	0.031 ± 0.004	1.0
8	2	0.049 ± 0.008	∞	0.970 ± 0.007

Results

Maximum likelihood estimates of the tag-shedding parameters and of their standard errors are given in Table 3. Curves, based on these parameter estimates, that describe the time-dependent probability of tag shedding, together with estimates of the proportion of tags lost (with 95% confidence intervals) based on grouped data, are shown in Figure 1.

In experiment 1, it proved impossible to distinguish either statistically or visually between a constant-rate model with immediate tag shedding (model 2) and a decreasing-rate model with no immediate tag shedding (model 3). Although the plots of $[1 - Q(t)]$ against t (Fig. 1a) are strikingly different for longer recapture times, apparently both can be accommodated by the grouped recovery data because the number of long-term recoveries is small, resulting in wide confidence intervals for proportions shed.

In all other experiments, it was possible to select a single most appropriate model on statistical grounds. However, wide confidence intervals for the estimates of proportions of tags shed were still evident in most experiments for the longer-term recovery periods. In experiment 2 and the medium-term experiments (4 and 6), a constant-rate model with some immediate tag shedding was selected (Fig. 1b, d, f). In the other long-term experiments (3 and 5), model (3) provided the best fit, and the shedding rate showed a marked tendency to decrease with time (Fig. 1c, e).

The most striking difference among the experiments was the very low shedding rates observed in experiments 7 and 8 (Fig. 1g, h) compared with the other experiments. After 4 years, the probability of shedding, as predicted by the fitted models, was approximately 0.2 for experiments 7 and 8, whereas it was 0.5–0.7 for the earlier experiments.

Discussion

The tag-shedding rates estimated for experiments 1–6 are of a similar order to those obtained for southern bluefin tuna by Kirkwood (1981), who used a restricted subset of the data pooled across these experiments. Constant rates of tag shedding have been estimated by Hynd (1969) for southern bluefin tuna (0.26/yr), by Bayliff and Mobrand (1972) for yellowfin tuna (0.278/yr), and by Lenarz et al. (1973) and Baglin et al. (1980) for Atlantic bluefin tuna (0.210/yr and 0.205/yr, respectively). The essentially constant rates estimated in this paper for experiments 2, 4, and 6 are generally slightly lower then these, but still comparable. However, the shedding rates estimated for experiments 7 and 8 are very much lower than for any previously reported tuna double-tagging experiment with substantial numbers of recoveries. The low estimates of shedding rates obtained by Laurs et al. (1976) for north Pacific albacore and Lewis (1981) for south Pacific skipjack were based on very small numbers of tag recoveries.

As mentioned earlier, most previous estimates of tag-shedding rates have been calculated using recovery data grouped by period at liberty. For this method to be effective, the number of observations in each grouping interval must be above a certain minimum. Where the data are sparse, the grouping intervals must cover longer periods. This can result in loss of information, as is seen, for instance, in Table 1 for the longer periods at liberty. Worse, as Kirkwood and Walker (1984) found for a double-tagging data set with very few recoveries, the grouped data estimates may be highly dependent on the grouping intervals used. Here, building on Kirkwood and Walker (1984), we have adopted an estimation procedure that uses exact periods at liberty, which—at least in principle—gets around this problem. However, this is not achieved without a price:

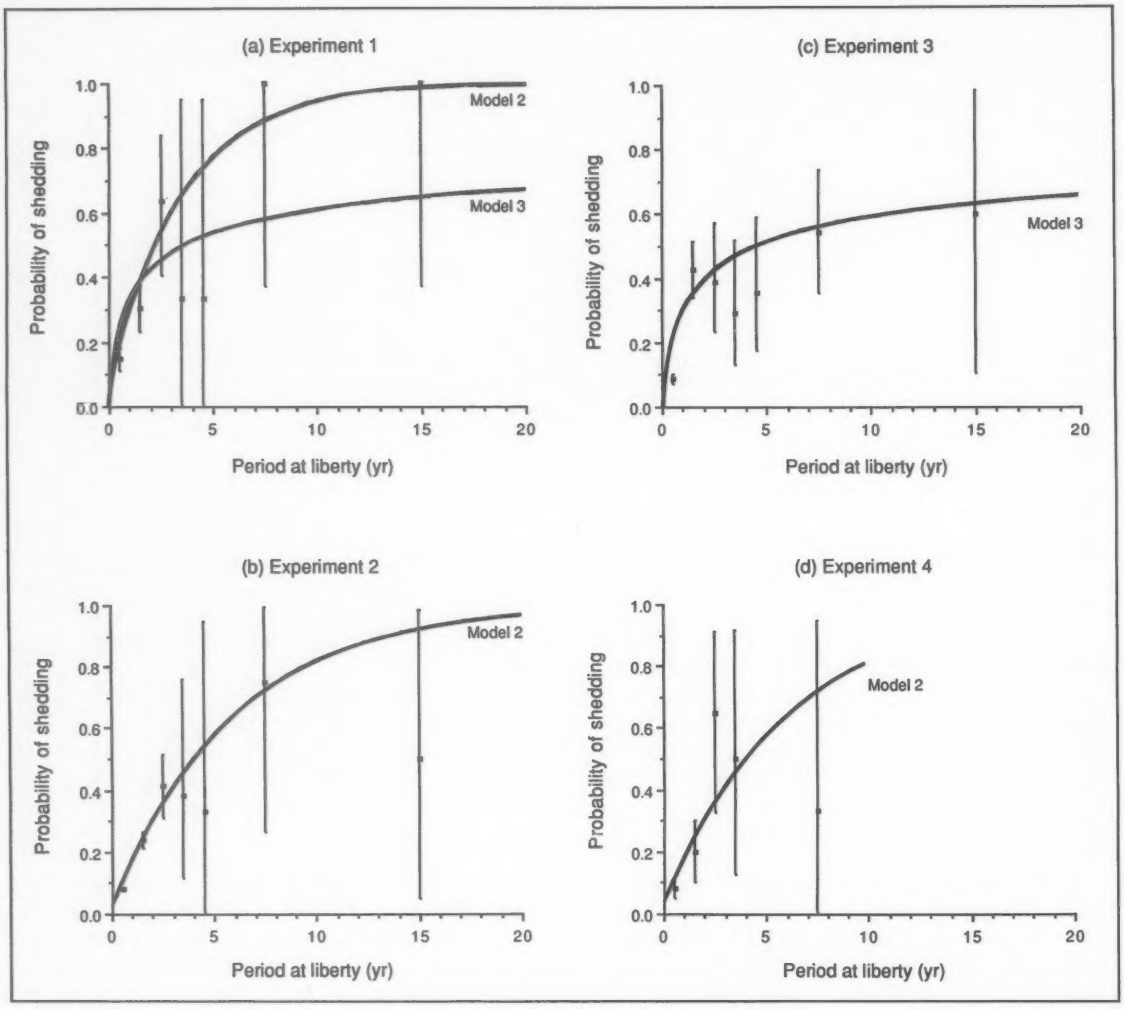

Figure 1

Comparisons of the probabilities of tag shedding by southern bluefin tuna as predicted by the best fitting models, with the proportions of tags shed as calculated from grouped data. Bars represent 95% confidence intervals on the proportions.

having to condition on the observed times at liberty, the calculated standard errors of the estimated parameters are almost certainly biased downwards. As the numbers of recaptures increase and the grouping intervals shorten, estimates based on grouped and ungrouped data should converge. However, the rate of convergence may be slower than might be expected. Table 4 gives parameter estimates that were calculated by applying the Kirkwood (1981) method to the grouped data in Table 2. Comparison of estimates using ungrouped data (Table 3) and grouped data (Table 4) reveals substantial differences, not only in terms of the parameter estimates themselves (e.g., experiments 3 and 5) but even in the model selected (e.g., experiments 6 and 7), despite the relatively large numbers of recaptures.

No formal statistical analysis is needed to conclude that the shedding rates in experiments 7 and 8 are significantly lower that those in experiments 1–6. We believe that the most likely explanation for these reduced shedding rates lies in differences in tags and tagging methods. Some of the tags used in the early experiments were reported to have inadequately attached streamers (Hynd et al. 1967). If so, this would

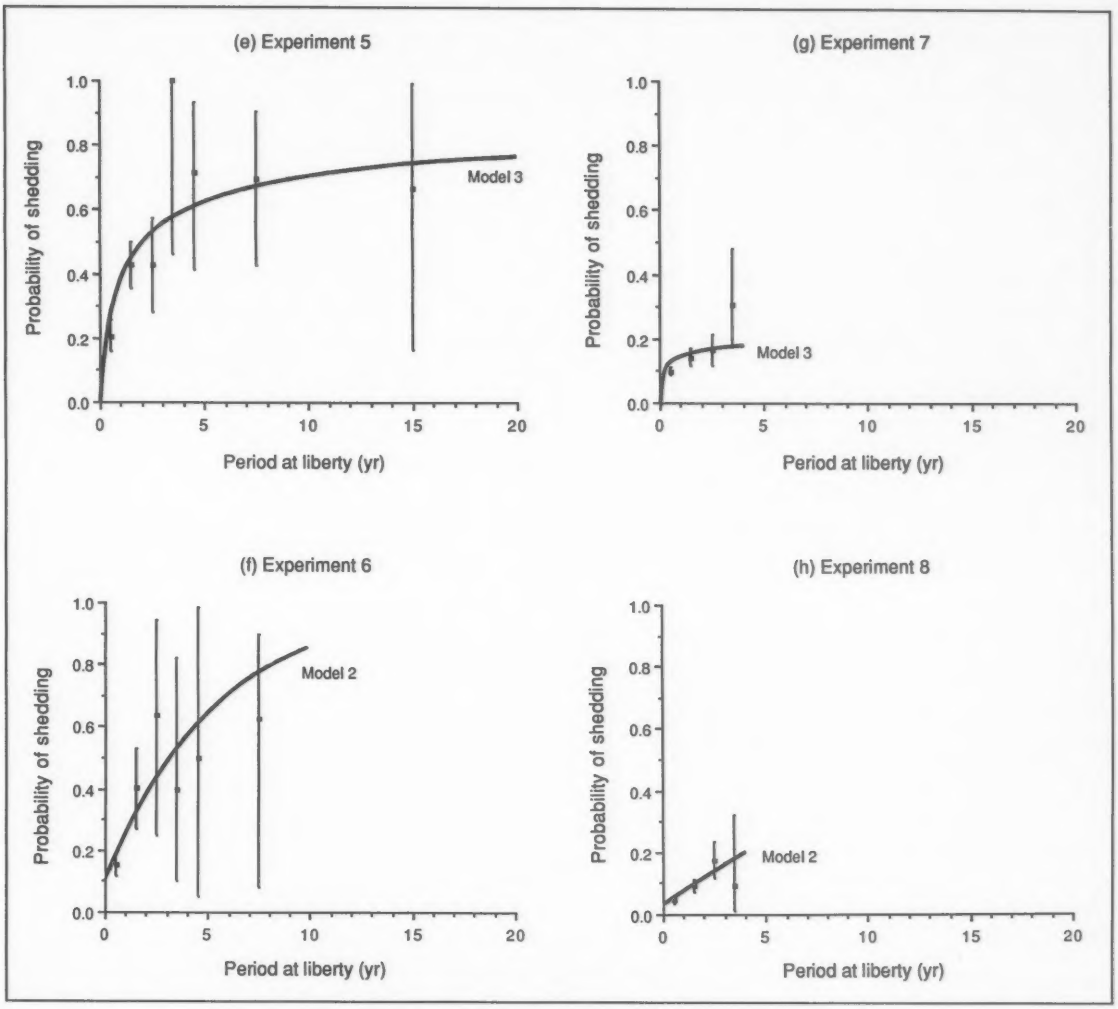

Figure 1 (continued)

Table 4

Maximum likelihood estimates of tag-shedding parameters for southern bluefin tuna double-tagging experiments using grouped data.

Experiment no.	Selected model	Parameters		
		$\lambda \pm SE$	$\beta \pm SE$	$\rho \pm SE$
1	2	0.26±0.05	∞	0.98±0.05
2	1	0.18±0.01	∞	1.0
3	3	0.27±0.07	0.55±0.37	1.0
4	1	0.20±0.04	∞	0.96±0.01
5	3	0.56±0.14	0.66±0.32	1.0
6	3	0.43±0.09	0.53±0.27	1.0
7	2	0.053±0.010	∞	0.93±0.01
8	2	0.055±0.011	∞	0.98±0.01

result in a higher rate of shedding. Tags used in the latest experiments do not appear tc have suffered from such defects. In experiments 7 and 8, the use of a specially designed tagging cradle may have resulted in more effective and less traumatic tagging than in earlier experiments, where fish were tagged on a measuring board. Also in experiments 7 and 8, a deliberate effort was made to anchor the tags behind the second dorsal fin ray extensions. Tags successfully attached in this way should have a very small probability of shedding. Unfortunately, little quantitative information is available on the efficacy of the technique of tag attachment adopted for experiments 1–6, but it is known that greater care was taken in tag attachment in the later experiments. If the proportion of ideally attached tags in experiments 1–6 differed markedly from those for experiments 7 and 8, then commensurate differences in shedding-rate estimates would result.

While the lower tag shedding rates in experiments 7 and 8 are obvious on first inspection, the situation is less clear for the earlier experiments. In general terms, the precision of estimates of shedding rates, particularly long-term rates, will increase with the size of the database. On these grounds, pooling of the data for experiments 1–6 would appear to be an attractive option. However, it would be appropriate to do so only if the assumptions underlying the analysis of the pooled data remained valid. Critical among these assumptions is that all tags have identical and independent shedding probabilities. The primary reason for classifying the tag releases in the 1960s and 1970s as six separate experiments was a suspicion that these probabilities may well have been heterogeneous. As mentioned earlier, with this classification we were attempting to minimize within-experiment differences in geographical area, fish size, capture and tagging methods, and tagging personnel. While in principle further subdivision is possible, for example by tagging vessel in order to take account of different tagging teams, we felt this may leave too few data in each subset to obtain reliable estimates of shedding rates. Also, no assertion is made that the classification chosen is an optimal one; indeed it is by no means obvious that suitable criteria for optimality could be defined. A statistical way of examining whether or not it is appropriate to pool data for experiments 1–6 is to carry out a likelihood ratio test of the hypotheses that the tag shedding parameters for each experiment are equal. This hypothesis proved to be resoundingly rejected ($P<0.001$). It appears that pooling is not a viable option for these experiments.

One of the subsequent analyses that we had envisaged for recovery data adjusted for tag shedding involved application of the method of Hearn et al. (1987) to obtain estimates of natural and fishing mortality rates. This method, which is essentially a cohort analysis of the tagging data, gives particular weight to long-term recaptures and therefore requires accurate estimates of long-term shedding rates. Despite the large numbers of recoveries in the experiments described in this paper, precise estimation of long-term shedding rates has not been possible. This is best exemplified in the results of experiment 1, where no single best fitting model was obtained, and for which the point estimates of long-term shedding rates differ markedly. Even where a single best-fitting model was available, considerable uncertainty still remained about the long-term shedding rates. It therefore seems essential to take account of this uncertainty in any subsequent analyses using methods such as that of Hearn et al. (1987). This is the subject of further research.

Acknowledgments

Dr. G. Eckert, Dr. V. Mawson, and Ms. S. Wayte reviewed and provided helpful comments on an earlier draft of this manuscript. We also thank Dr. W.S. Hearn for useful comments and discussion, particularly in relation to the assumption of independent and identical shedding rates.

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Ocean Stability and Anchovy Spawning in the Southern Benguela Current Region

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Abstract.—Seasonal advection of warm western-boundary current water into the southern Benguela eastern-boundary current region from late spring to early autumn coincides with increased coastal upwelling activity. The combined effect of these two processes is to stabilize the system through intensification of temperature fronts and thermoclines, providing conditions favoring anchovy spawning and larval survival. These conditions appear to be robust to short periods of intense storm mixing and downwelling during summer, and weaken and disappear only with the onset of winter when there is diminished influence of the warm western-boundary current water, downwelling conditions, and increased frequency of storms.

Manuscript accepted 24 November 1989.
Fishery Bulletin, U.S. 88:323–338.

The extension of the Hjort (1914) hypothesis by Lasker and his coworkers (Lasker 1975, 1978, 1981a, b) to include the role of a stable ocean in determining fish recruitment has had a profound influence on research into the early life history of marine fish. Lasker's extended hypothesis suggests that ocean stability influences food aggregations for larvae and larval drift and, hence, recruitment strength (Lasker 1981b). In support of Lasker's hypothesis, strong wind events have been found to disrupt anchovy larval food aggregations, and, by inference, to effect larval mortality off California (Lasker 1975) and Peru (Walsh et al. 1980). During such events, larvae can also be entrained within increased offshore Ekman flow and placed outside suitable feeding areas (Walsh et al. 1980, Lasker 1981b). A significant linear relationship between anchovy larval mortality rate and the frequency of calm, low wind-speed periods during the spawning season off California (Peterman and Bradford 1987) provides further evidence of the importance of event-scale disruption of ocean stability.

Parrish et al. (1983) compared the seasonality and geography of sardine and anchovy reproduction in the California, Peru, Canary, and Benguela Current systems with corresponding features of the environment and suggested that patterns of correspondence may indicate the most crucial processes affecting reproductive success. They found that spawning was adapted to avoid times and places characterized by intense turbulent mixing and strong offshore transport.

In this paper we use survey data to provide a finer-scaled description of ocean stability and anchovy spawning than that of Parrish et al. (1983), and suggest that in the southern Benguela Current system anchovy spawning is adapted to seasonal patterns of ocean stability that are resistant to event-scale processes. Local conditions are briefly compared with those in the Southern Californian Bight where Lasker's studies took place, and conclusions are drawn with respect to the influence of ocean stability on survival of the planktonic stages and recruitment in the southern Benguela Current region.

Methods

During the Cape Egg and Larval Programme (CELP), plankton and the environment were sampled at approximately monthly intervals between August 1977 and August 1978 from a grid of stations in the southern Benguela Current region. The purpose of the program was to determine general spawning habitat and time for the major fish species of commercial importance (Shelton 1986). The grid comprised 120 stations posi-

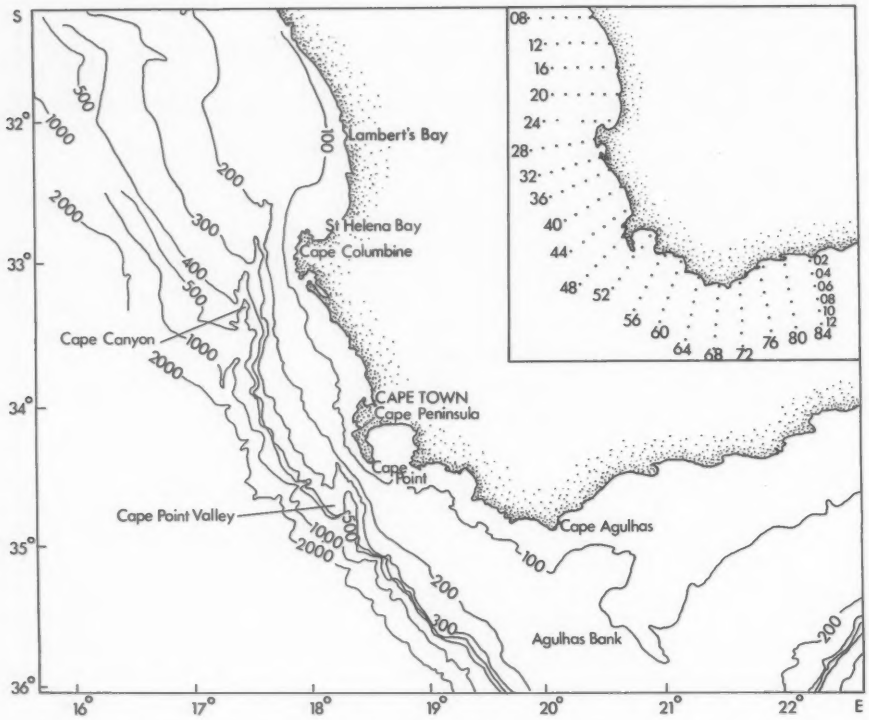


Figure 1

Cape Egg and Larval Programme (CELP) survey grid, southern Benguela Current region, sampled monthly August 1977–August 1978, and general topography of the survey area (depth contours in meters).

tioned at 10-nautical-mile intervals (18.5 km) on 20 transects (Fig. 1).

Vertical profiles of temperature and water samples for measurement of salinity, chlorophyll-*a* concentration, and microplankton density were collected from the water column. Chlorophyll analysis, described in Shannon et al. (1984), was by means the standard photometric method of SCOR/UNESCO Working Group 17 (1966). Microplankton particle concentration was determined by prefiltering 2 liters of the water sample through a 100-μm filter and collecting those particles retained by a 37-μm filter. Particles between 37 and 100 μm correspond to the size fraction considered to be important for first-feeding anchovy larvae (Arthur 1976, Hunter 1977). Particles were counted under a light microscope at 20× magnification and expressed as number per liter. Although all particles were enumerated, only the maximum density at each station of total "esculent" (nutritious to fish larvae [Sharp 1980]) particles are presented, such as copepod eggs, nauplii, copepodite stages, and dinoflagellates. Wind strength and direction were estimated by the lighthouse keeper at Cape Point throughout the period. In order to examine surface drift patterns, 20 plastic drift cards (Duncan 1965) were released monthly at each station sampled.

Fish eggs and larvae were sampled by means of a double oblique haul of a Bongo sampler down to a maximum depth of 100 m. The sampler had a mouth opening of 57 cm and was fitted with 300-μm and 500-μm mesh nets. Counts of anchovy eggs and larvae from the 300-μm unit were standardized to volume or numbers under 10 m^2 using the formula given in Smith and Richardson (1977). In November 1979 and November 1984 the vertical distribution of anchovy eggs and temperature profiles was measured at two localities. Eggs were sampled with Miller nets (Miller 1961) as described in Shelton and Hutchings (1982). Anchovy egg and early-stage larval abundance data from a more extensive grid of stations sampled in November 1983 using a CalVET net (Smith et al. 1985) are also presented.

Results and discussion

Seasonality in temperature and spawning

Both the mean and the coefficient of variation (CV) of sea surface temperature measured over the CELP grid peaked in summer (Fig. 2). This is caused by the seasonal advection of warm water orginating from the western-boundary Agulhas Current into the southern Benguela Current region (Shelton et al. 1985) and the simultaneous increase in coastal upwelling (Andrews and Hutchings 1980). Strong cross-shelf temperature gradients, or fronts, are set up between advected and upwelled water, reflected by the increase in the surface temperature CV. In winter the influence of western-boundary current water is diminished and upwelling is less frequent and less intense (Shelton et al. 1985, Andrews and Hutchings 1980). Consequently, cross-shelf temperature gradients weaken and disappear and mean SST values are lower and have a lower CV, reflecting cool, more isothermal conditions.

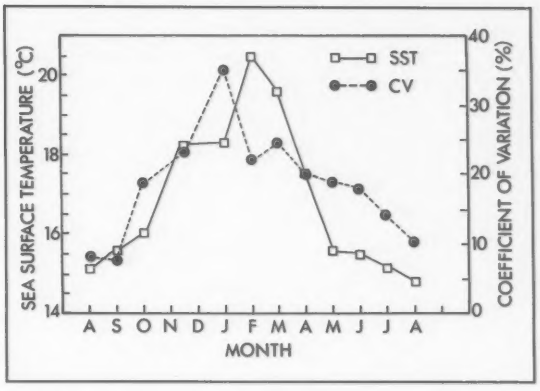


Figure 2

Monthly means and coefficents of variation (CV) of sea-surface temperature (SST) values over the CELP survey grid, southern Benguela Current region, for the period August 1977–August 1978.

Horizontal structure

The changes in temperature structure described above, as well as associated changes in the patterns of abundance of microplankton and chlorophyll-*a*, can be seen in contour diagrams of values for summer and winter (Fig. 3). The strong temperature front that develops along the west coast in summer is clearly visible. Although this front is most persistent between Cape Point and Cape Columbine, and was considered by Bang (1973) to "pivot" at Cape Point, it may extend as far south as Cape Agulhas when upwelling occurs at capes east of Cape Point. At Cape Columbine isotherms tend to diverge offshore, and further north the front is generally weaker and more variable. The density of potential food particles for early-stage larval feeding, as indicated by microplankton and chlorophyll-*a* concentrations, are highest inshore of the temperature front in summer, indicating that the front constrains the offshore Ekman drift of productive upwelled water. In winter when the front disappears, microplankton and chlorophyll-*a* concentrations are generally lower and more dispersed.

Arrows indicating major directions of surface drift over the survey area in summer (January 1978) and winter (August 1977) based on drift-card recoveries are plotted in Figure 4. Of the 24,000 cards released in each month there was a 5% recovery in January 1978 and a 7% recovery in August 1977. There was no clear seasonality in the overall recovery rate. In summer the southern Agulhas Bank area was characterized by onshore surface flow with a westerly component. Some cards released over the western Agulhas Bank moved around Cape Point and up the west coast, and the general pattern of flow inshore of the strong temperature front on the west coast was northwards. North of Cape Columbine there was some evidence of onshore flow. There were very few southern African recoveries offshore of the front, although several cards were recovered along the eastern coast of South America, indicating general offshore flow into the South Atlantic gyre at stations offshore of the front.

In winter, flow in the south was again predominantly onshore, although this time with a marked easterly component east of Cape Agulhas and a westerly component to the west. Several cards released on the western Agulhas Bank were found substantial distances up the west coast, although one card released in the extreme north of the grid travelled against this flow and was recovered on the east coast. Again, few cards were recovered on the coast of southern Africa from releases on the west coast, although there were 10 recoveries from the coast of South America and one recovery from southern California. In comparison with summer, several of these recoveries came from cards released at inshore stations, indicating widespread offshore flow along the west coast in the absence of the front.

Vertical structure

Summer and winter vertical structure of temperature, microplankton density, and chlorophyll-*a* concentration are shown for three representative sections over the survey area in Figures 5–7. A section over the Agulhas Bank (Fig. 5) shows the existence of a strong thermocline in summer between warm water of Agulhas

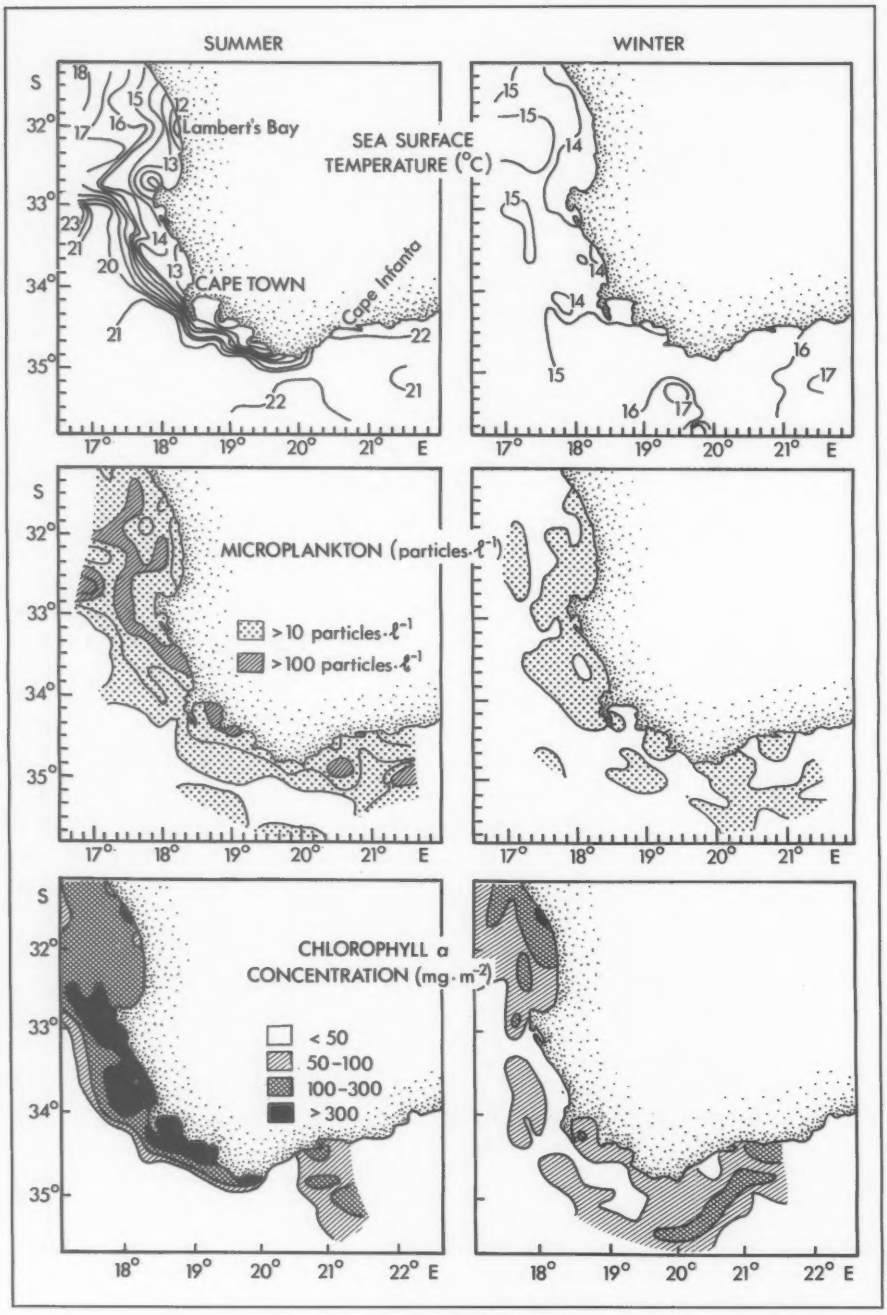


Figure 3

Typical summer (January 1978) and winter (August 1977) patterns of sea-surface temperature, microplankton particle concentrations, and chlorophyll-*a* concentrations over the CELP survey grid, southern Benguela Current region.

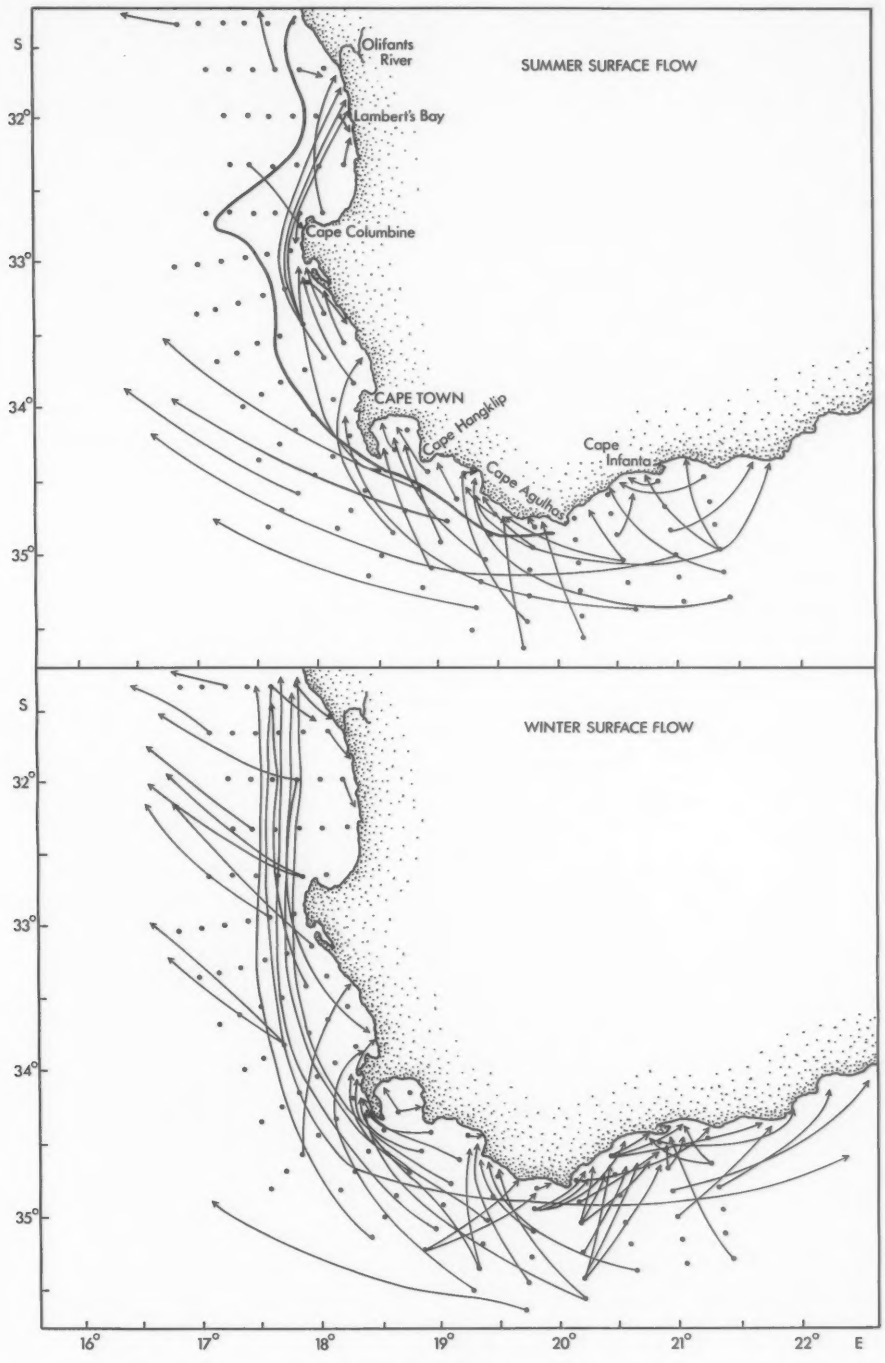


Figure 4

Summer and winter patterns of surface flow in the southern Benguela Current region, gauged from drift-card recoveries from releases of 20 cards at each station in January 1978 and August 1977. Arrows may represent more than one recovery and indicate general direction of flow.

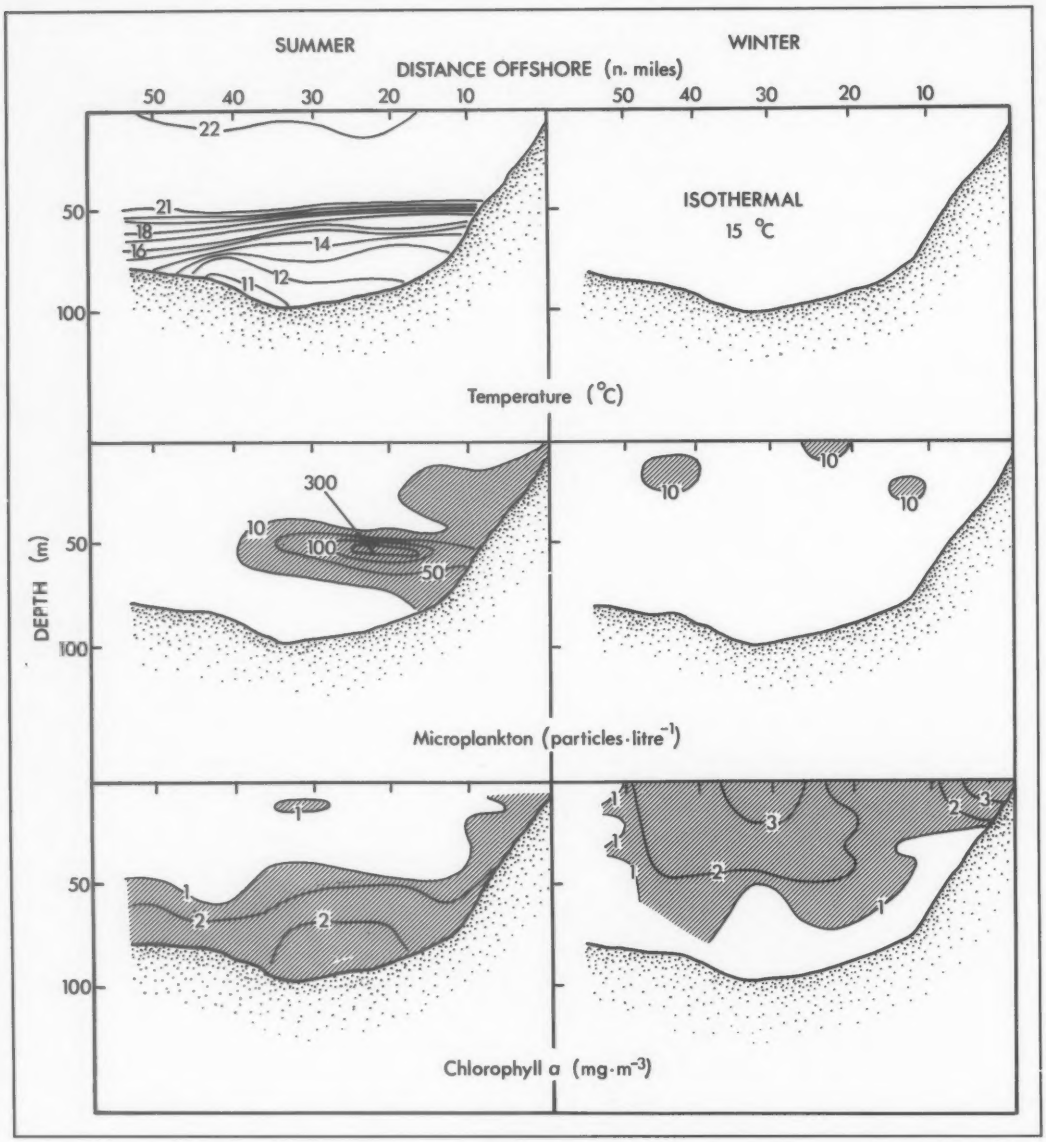


Figure 5

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 76 over the Agulhas Bank, southern Benguela Current region.

Current origin forming an upper mixed layer and cold water that moves onto the Bank along the bottom in summer. The warm layer had very low plankton densities, but enhanced microplankton density and phytoplankton-*a* concentration were associated with the thermocline.

With the onset of winter, the influence of the warm Agulhas Current water over the Agulhas Bank becomes less and heat loss to the atmosphere increases, causing a cooling of the surface layer. Surface cooling combined with the movement off the shelf of the cold bottom layer makes the water column less stable and susceptible to mixing by winter storms (Shannon et al.

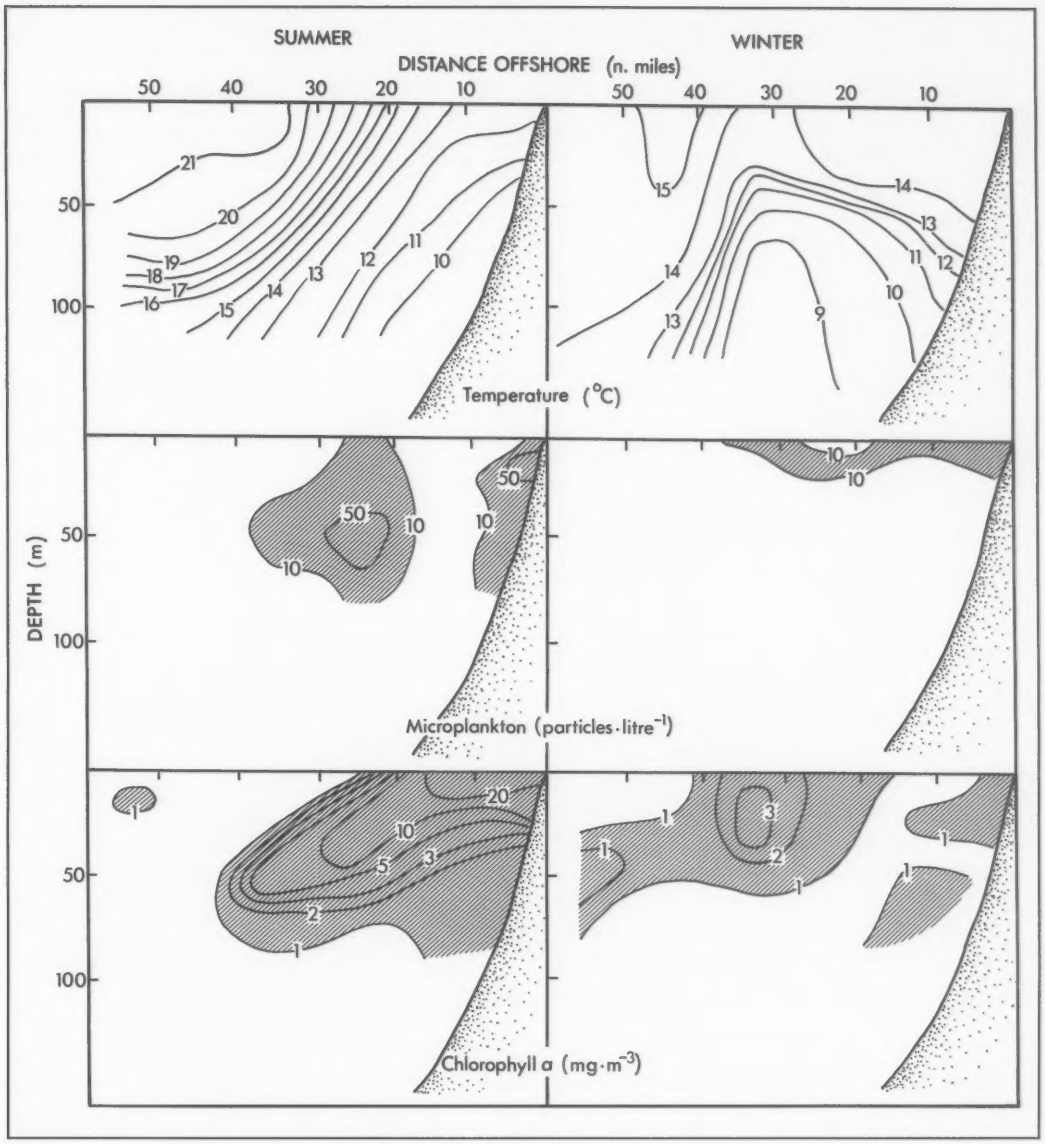


Figure 6

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 44 just north of Cape Town, South Africa.

1984, Largier and Swart 1987). Microplankton particle concentrations tend to be low in the well-mixed water column but chlorophyll-*a* concentrations can be quite high, either if nutrients accumulated in bottom sediments are mixed into the euphotic zone by strong storm action (Shannon et al. 1984), or if periods of calm weather persist long enough for the water column to stabilize, albeit weakly, and phytoplankton is thereby allowed to remain in the euphotic zone long enough to grow.

A section just north of Cape Town (Fig. 6) shows the strong temperature front in summer between cold upwelled water inshore and warm water offshore. Enhanced levels of microplankton occurred in the vicinity

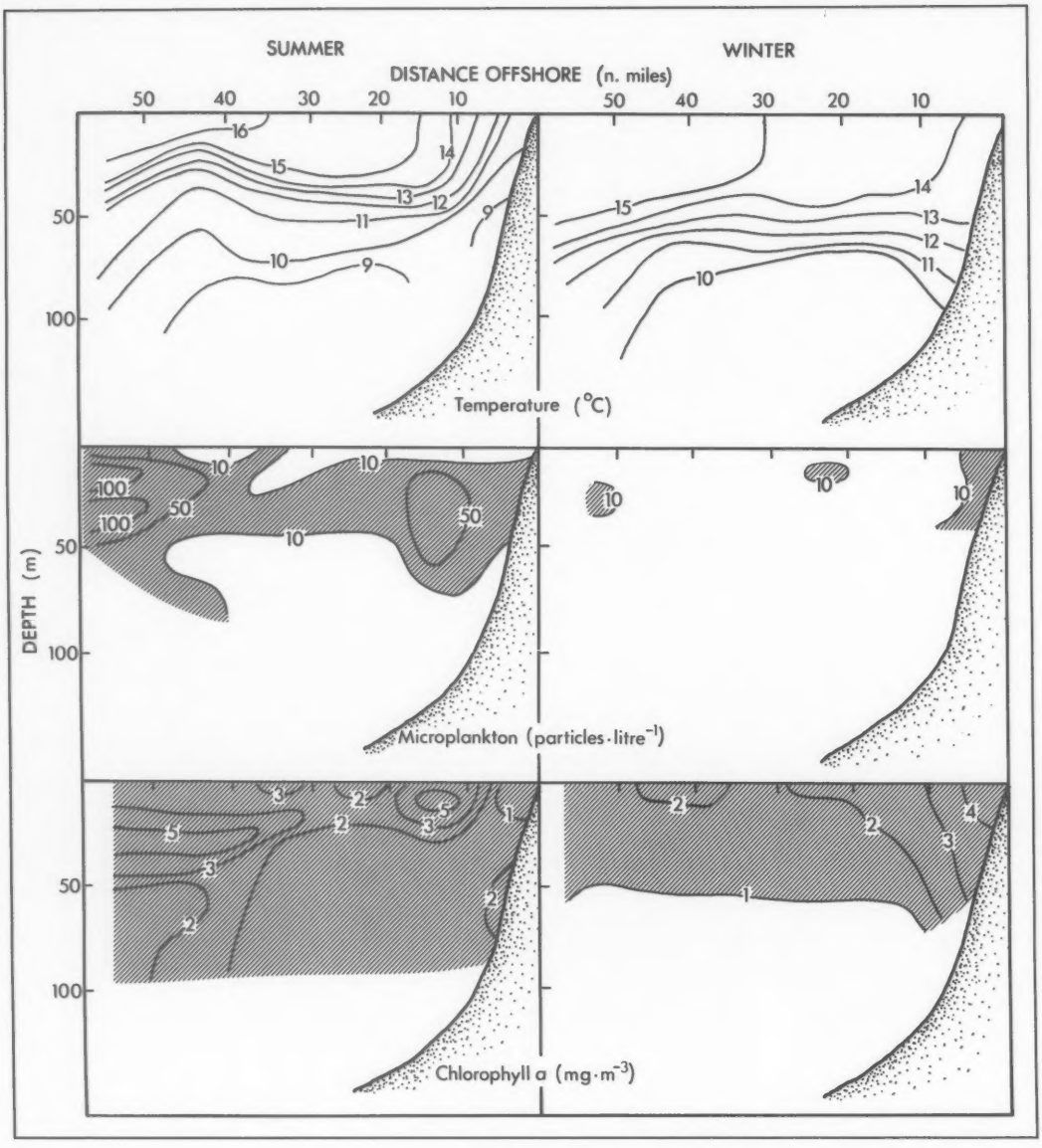


Figure 7

Summer (January 1978) and winter (August 1977) sections of temperature, microplankton, and chlorophyll-*a* values along line 16 in the vicinity of Lambert's Bay, South Africa.

of the front as well as close inshore, and high levels of chlorophyll-*a* were found inshore near the surface, declining in concentration and following the isotherms into deeper water in the vicinity of the front. Offshore of the front, both chlorophyll-*a* and microplankton levels were negligible. A similar pattern was noted in a transect of the front off Cape Columbine in December 1984, with copepod nauplii and copepodites concentrated in the front and chlorophyll-*a* values increasing towards the coast, inshore of the front (Armstrong et al. 1987). Although the front may persist as a subsurface feature in winter, even during prevalent downwelling conditions, it is much weaker as a consequence of cooler water offshore. Microplankton and chlorophyll-*a*

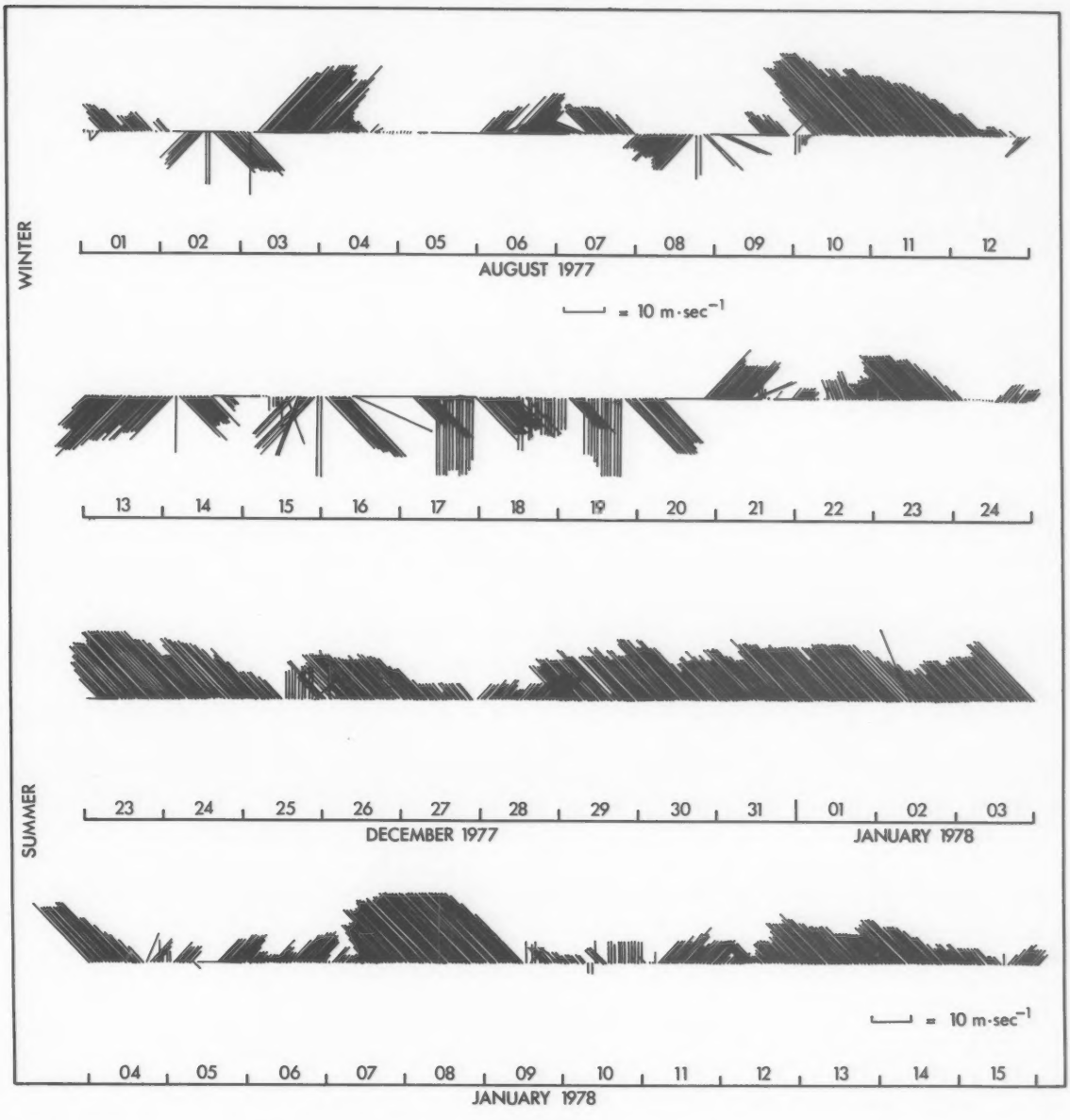


Figure 8

Wind stick diagram for the period 23 December 1977–15 January 1978 and 1–24 August 1977, showing tyical summer and winter patterns of wind stress measured at the lighthouse at Cape Point, South Africa.

values are generally much lower and more dispersed over the west coast between Cape Point and Cape Columbine in the absence of the surface front in winter.

A section on the west coast off Lambert's Bay (Fig. 7) shows a moderately strong thermocline with coastal upwelling in summer. Moderate-to-high levels of microplankton and chlorophyll-*a* extending to the limit of the grid in the top 50 m are typical of the area at this time. In winter the thermal structure is similar, but with less upwelling activity and cooler water offshore. Although microplankton levels were low in the section shown, widespread moderate levels of chlorophyll-*a* are quite

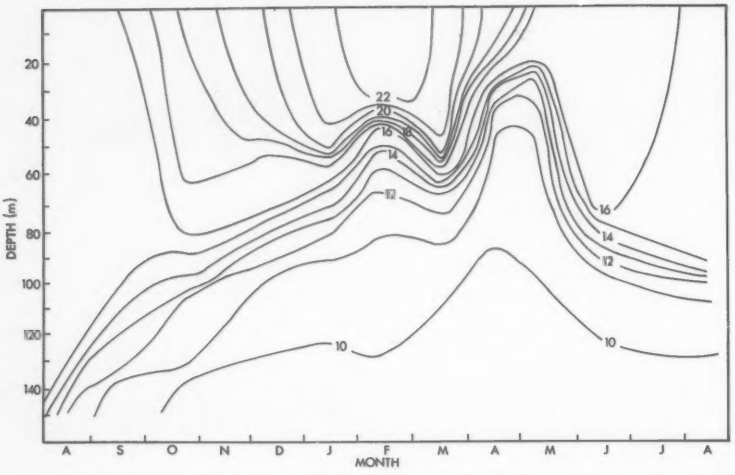


Figure 9
Variability in the vertical temperature structure at station 64–06 on the Agulhas Bank, southern Benguela Current region.

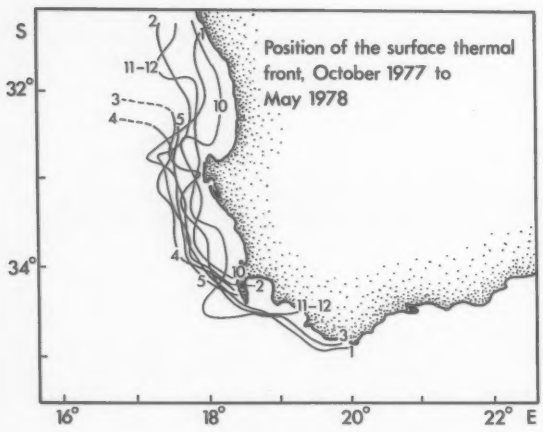


Figure 10
Variability in the position of the surface temperature front in the southern Benguela Current region, spring 1977 through autumn 1978. (Numbers refer to months of the year, e.g., 10 = October 1977, 2 = February 1978.)

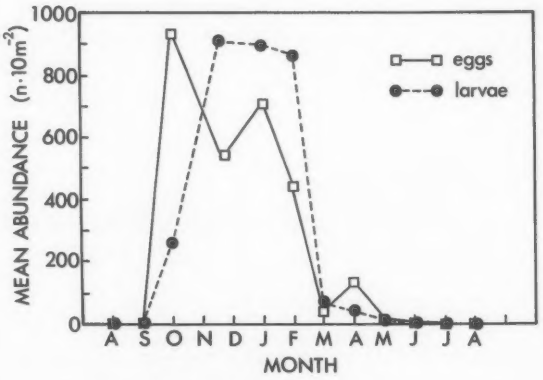


Figure 11
Monthly mean abundance of anchovy eggs and larvae over the CELP survey grid, southern Benguela region, for the period August 1977–August 1978.

typical for the recruitment area in winter, as shown in Figure 3.

Robustness to event-scale processes

Wind stick diagrams of wind strength and direction estimated by the lighthouse keeper at Cape Point (Fig. 8) show that winter is characterized by frequent periods of strong northerly wind interspersed with southerly winds and calm, whereas in summer strong upwelling-favorable southeasterlies dominate, alternating with brief periods of calm and occasional wind reversals. Despite event-scale forcing of this nature, contoured monthly temperature profiles through the water column over the Agulhas Bank show strong stratification persisting over several months of the spring-to-autumn period, weakening and disappearing with the onset of winter (Fig. 9). Similarly, although erratic in appearance and position to the north and south, the temperature front in the transport area between Cape Point and Cape Columbine persists as a stable feature for up to 8 months of the year (Fig. 10), despite event-scale variability in the wind field. During lulls in upwelling the front may weaken at the surface and move inshore, at which time the temperature discontinuity may be most apparent in the form of a thermocline, but it persists as a subsurface feature further offshore (Shelton

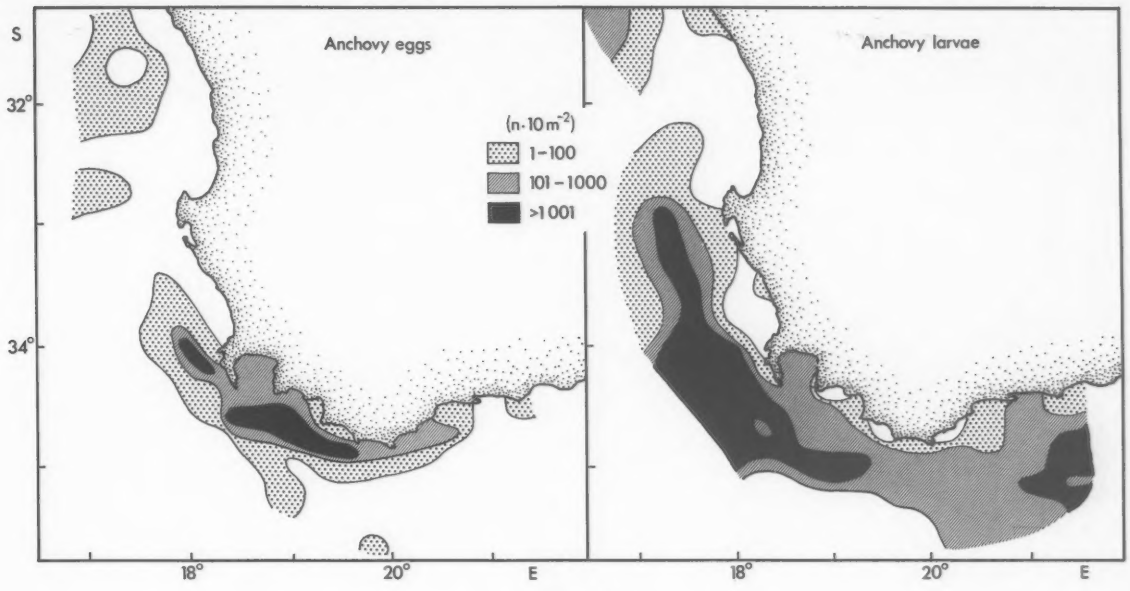


Figure 12

Anchovy egg and larval abundance patterns over the CELP survey grid, southern Benguela Current region, in January 1978, a month of peak spawning.

1986). With the next pulse of upwelling, the isotherms flip to a more vertical orientation and the front moves offshore again, to an average position over the inner shelf break (200-m contour).

Anchovy spawning, transport, and recruitment in relation to ocean stability

Anchovy eggs are generally absent or in very low abundance in the plankton in autumn and winter when the region is cool and isothermal (March–August, Fig. 11). With the onset of spring (September–November) both egg and larval abundance increases rapidly, reaching a peak in late spring or early summer when both the mean temperature and the CV are high, and then decreasing to low numbers over the autumn.

Anchovy spawning is typically most intense south and east of Cape Point over the broad Agulhas Bank (Fig. 12). The vertical distribution of anchovy eggs in the spawning area on the Agulhas Bank (Fig. 13a) is restricted almost entirely to the warm upper mixed layer, above the strong thermocline that forms in summer at about 50 m. On the west coast a transect bisecting the front in the vicinity of the Cape Peninsula shows that anchovy eggs extending up the west coast are concentrated within the frontal zone (Fig. 13b). Anchovy larvae (Fig. 12) are generally more widespread over the Agulhas Bank than the eggs as a result of dispersal, and in particular extend further up the west coast, often as far as Cape Columbine, in the vicinity of the front. Recent samples from a more extensive grid of stations confirm these patterns (Fig. 14).

Based on these patterns of anchovy eggs and larval abundance and the catch pattern of recruits in the commercial fishery (Crawford et al. 1980 and Crawford 1980), the habitat of the anchovy in the southern Benguela region can be divided into spawning, transport, and recruitment areas (Fig. 15). The role of ocean stability in each of these three areas can be evaluated.

Anchovy spawning is highly seasonal, peaking in summer when the southern Benguela region is most structured by temperature fronts and thermoclines under the simultaneous influence of advected warm western-boundary current water and coastal upwelling. The spawning area is characterized by a strongly stratified, stable water column throughout summer. Stratification is resistant to event-scale mixing processes and only weakens with the reduced influence of eastern-boundary current water on the Bank and the retraction of the cold bottom layer with the onset of winter. Winter storms are then able to mix the entire water column creating isothermal conditions which persist until the onset of summer. The warm, uniform surface layer over the Agulhas Bank in summer provides conditions conducive to rapid anchovy egg development; below 14°C anchovy egg development in the

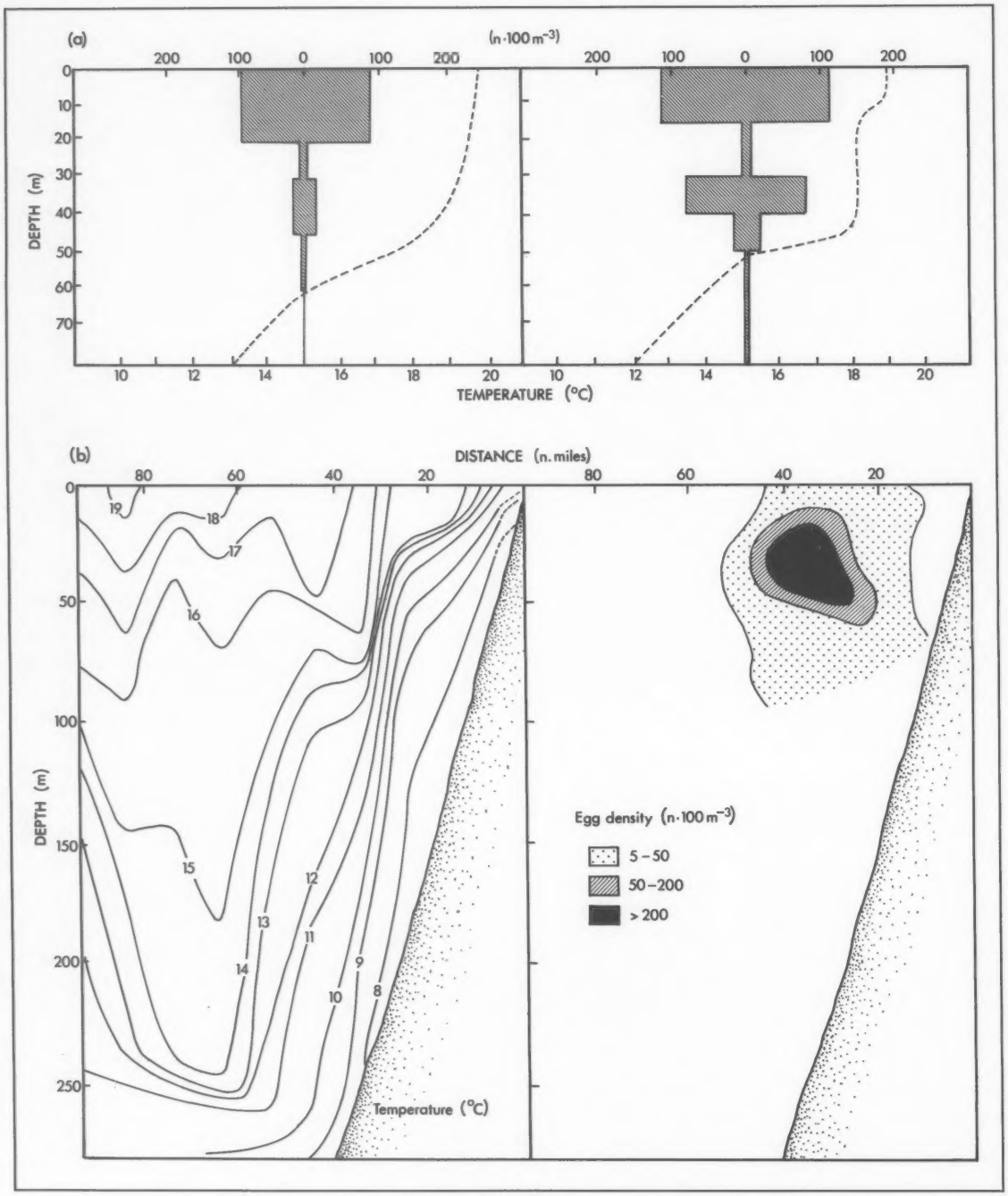
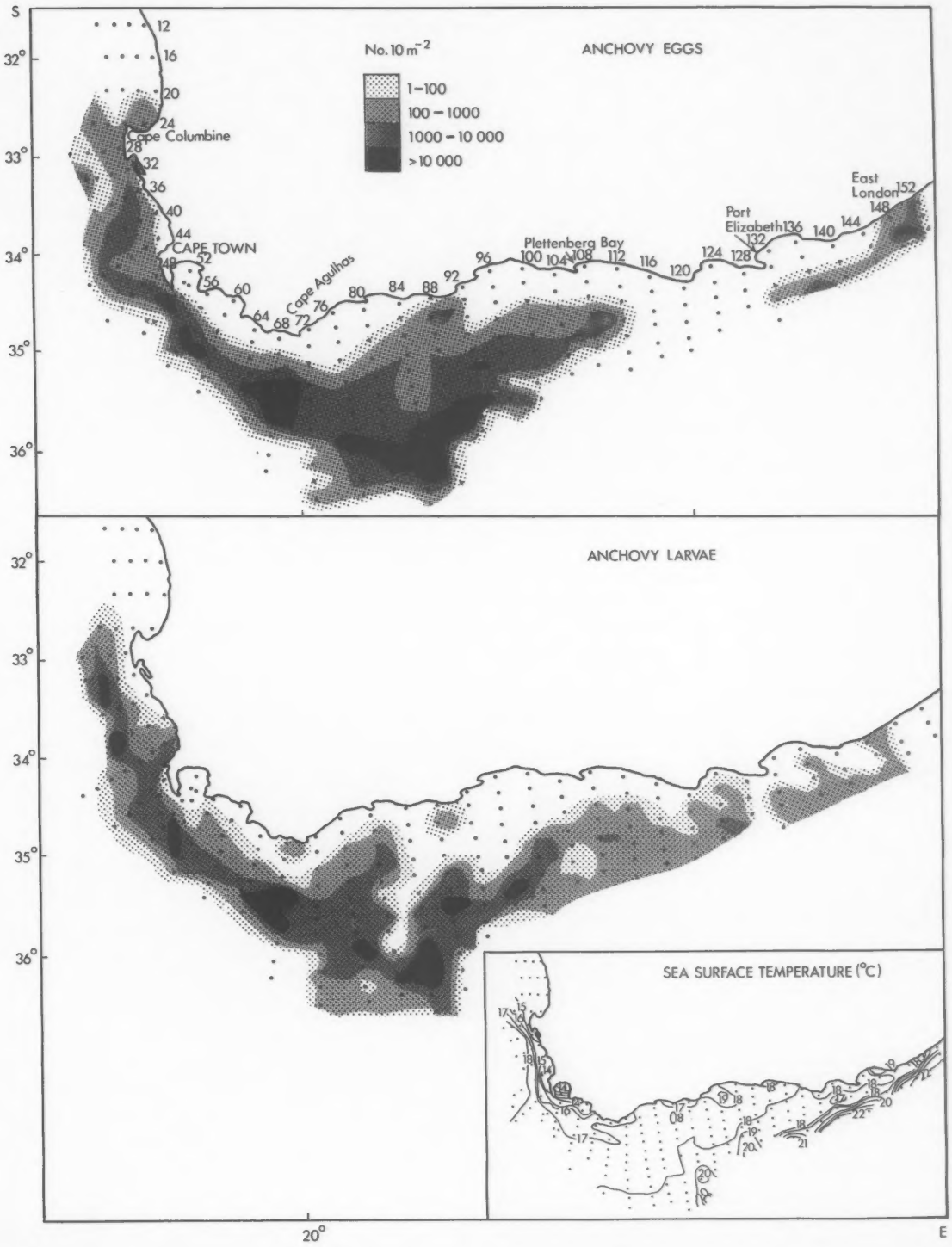


Figure 13

(a) Vertical distribution of eggs and temperature at depth for two stations in the anchovy spawning area, southern Benguela Current region, November 1984. (b) Vertical sections of temperature and anchovy egg abundance measured along a transect bisecting the temperature front off the Cape Peninsula, South Africa, November 1979.

Figure 14

Pattern of abundance of anchovy eggs and larvae in November 1983 from an extensive survey grid covering nearly the entire anchovy spawning area in the southern Benguela Current region.


S
32°
33°
34°
35°
36°
No. 10 m⁻²
1–100
100 – 1000
1000 – 10 000
>10 000
ANCHOVY EGGS
Cape Columbine
CAPE TOWN
Cape Agulhas
Plettenberg Bay
Port Elizabeth
East London
ANCHOVY LARVAE
SEA SURFACE TEMPERATURE (°C)
20°
E

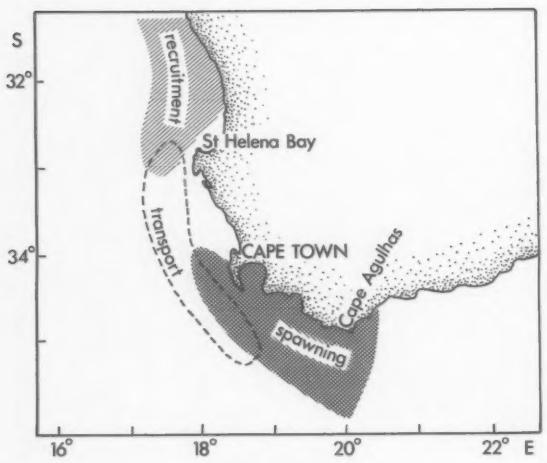


Figure 15
A generalized representation of anchovy spawning, transport, and recruitment areas in the southern Benguela Current region.

laboratory is very slow and hatching larvae are deformed (King et al. 1978). Below the warm surface layer a strong thermocline at about 50 m is associated with subsurface maxima of microplankton and chlorophyll-*a*, facilitating the survival of early-stage larvae that require high concentrations of food particles within a suitable size range (Lasker et. al. 1970).

Spawning conditions in the southern Benguela appear to be in marked contrast with conditions in the spawning ground of the Northern anchovy *Engraulis mordax* in the Southern California Bight where Lasker's studies were carried out. Surface temperatures in the Southern California Bight given in Lasker (1981b) are some 3–5°C lower than over the Agulhas Bank during the respective spawning seasons. Vertical temperature structure during the spawning season off southern California, as shown in Lasker (1978), is quite variable, with generally weak stratification susceptible to mixing. The chlorophyll-*a* layer disrupted by storm mixing in April 1984 was at about 15 m (Lasker 1975), in contrast to the deeper maxima on the Agulhas Bank. Although maximum chlorophyll-*a* values before storm mixing in the layer off California in April 1974 are similar to those recorded in the Agulhas Bank layer, microplankton particle concentrations over the Agulhas Bank do not reach the high values recorded by Lasker (1981b) because dinoflagellates are not as common as in the Southern California Bight, possibly due to persistent strong winds (Parrish et al. 1983), which thoroughly mix the relatively deep, upper mixed layer.

From the the spawning area in the south, the drift of eggs and early-stage larvae is primarily northwestwards, into the west coast transport area. Bang (1973) and Bang and Andrews (1974) have documented the presence of a strong northward-flowing jet current associated with the front which is a prominent feature of this area in summer. The role of this jet in transporting anchovy eggs and early-stage larvae from the Agulhas Bank spawning ground to the west coast nursery area has been examined and described in Shelton and Hutchings (1982). Drift-card recoveries for summer support their interpretation. In the transport area, enhanced levels of chlorophyll-*a* and microplankton associated with the inshore and frontal zone may be important in early-larval survival. Despite predominantly southeast winds in summer, facilitating offshore Ekman flow and upwelling at the coast, the offshore loss of eggs and larvae along the west coast may be small because of the constraining influence of the front. However, there is frequently an offshore divergence of the front off Cape Columbine, following the orientation of bottom contours, and this may be associated with the "leaking" of water containing larvae from the productive coastal region (Shelton et al. 1985, Shelton 1986).

Onshore flow north of Cape Columbine facilitates penetration of the productive recruitment area by larvae. Positioned downstream of the major sites of upwelling at Cape Columbine and Cape Point, the frontal structure dominating the transport area in summer gives way to more gently sloping isotherms north of Cape Columbine where the shelf widens. Because of lower average wind speeds (Hutchings et al. 1988), upwelling is milder than in the transport area and a vertically stable water column is a persistent feature. Enhanced levels of microplankton and chlorophyll-*a* characterize the inner shelf in this area throughout the year (Hutchings 1981), providing suitable conditions for the survival and growth of anchovy recruits.

The patterns of ocean stability described above, based largely on survey data, appear to have played a major role in shaping the spawning behavior observed by anchovy in the southern Benguela region. Upwelling generates the high levels of plankton production that support the spawning biomass of up to 2 million tons of anchovy estimated for the area (Armstrong et al. 1988), but the associated processes of turbulence and offshore Ekman flow present special problems to the plankton stages that have to be solved through evolutionary adaptation. In the southern Benguela region this appears to have been brought about by the selection of times and areas of spawning which make best use of seasonal and spatial patterns of ocean stability to provide suitable food concentrations and favorable transport.

Survey data for the southern Benguela therefore tends to confirm the conclusions from the larger-scale

comparative study of eastern-boundary currents by Parrish et al. (1983) that the spawning habits of anchovy (and sardine) attempt to minimize both wind-induced turbulent mixing and offshore-directed transport. Bakun (1985) argues that the results of Parrish et al. (1983) strengthen the relevance of Lasker's hypothesis to modeling recruitment and exploratory data analysis. However, if anchovy populations in the different eastern-boundary current regions have essentially "solved" the problems of disruptive turbulence and unfavorable transport, "mistakes" should be rare and difficult to find in the field. The fact that event-scale disruptive turbulence has been observed in the spawning area off southern California and that the incidence of calm periods can be statistically related to daily larval mortality rate (Lasker 1975, 1981b; Peterman and Bradford 1987) suggests that such "mistakes" do occur despite adaptations. Even so, they may be undetectable in recruitment measurements, either because of large and often unquantified measurement error, or because the "mistakes" are masked by a well-developed suite of "bet-hedging" traits (Shelton 1987). Estimates of anchovy recruitment (with error bars) for the southern Benguela population based on direct surveys (Butterworth 1989, Fig. 16) show less variability than anticipated in the literature (e.g., Beddington and Cooke 1983), although the time series is still too short to be conclusive.

If the southern Benguela anchovy population is adapted to local persistent patterns of ocean stability and is well-buffered against event-scale variations through bet-hedging, a prerequisite for detectably poor recruitment at moderate spawning stock sizes may be season-long weakening or disruption of the stability patterns in either the spawning, transport, or recruitment areas. Such conditions would probably arise if the influence of Agulhas Current water over the Agulhas Bank and on the west coast were reduced, particularly over the summer period.

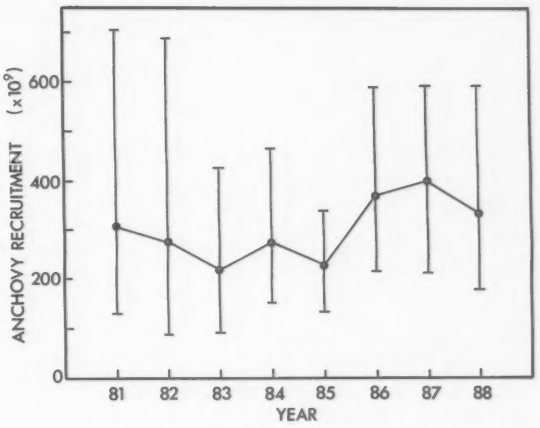


Figure 16

Estimates (median and 95% confidence interval) of annual anchovy recruitment for the southern Benguela population, deduced from direct survey results to July 1988 (Butterworth 1989).

Acknowledgments

We acknowledge the input of several of our colleagues at the Sea Fisheries Research Institute, Cape Town, to the Cape Egg and Larval Programme. In particular, Garth Newman and Vere Shannon provided much of the impetus for the initiation of CELP, and Alan Robertson, Hennie Crous, Frans Kriel, Deon Horstman, Donald Alexander, Robert Cooper, Gustav Wehmeyer, Jan Van der Westhuizen, Chris Jeenes, John Giddey, and Christine Illert gave excellent technical support during its execution. Colleagues at the NMFS Southwest Fisheries Center, La Jolla, particularly the group formally headed by Reuben Lasker, are thanked for their advice and encouragement with respect to the studies of anchovy early-life history in the Benguela Current system. We dedicate this paper to the memory of Reuben.

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Occurrence and Distribution of the Vaquita *Phocoena sinus* in the Northern Gulf of California

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Abstract.—A total 3236 km of boat and aircraft surveys was conducted in the northern Gulf of California in search of the vaquita *Phocoena sinus* in 1986–1988. Vaquita were seen on 51 occasions, representing an estimated 96 individuals. Forty-three porpoises (19 sightings) occurred during 1715 km of vessel transects, a rate of 2.51 individuals/100 km of surveys. The number of sightings relative to the extent of the survey emphasized the rarity of the porpoise and is a cause for concern regarding the vulnerability of the population. All sightings of vaquita occurred north of lat. 30°45'N, and all but two sightings (96.1%) occurred less than 40 km from San Felipe, Baja California Norte. Porpoises were observed in small groups (≤3 individuals) in all but five sightings. The mean group size was 1.9 ± 1.24 SD individuals, and the mode was 1. All sightings occurred in water depths of 13.5–37.0 m ($\bar{x}$ 26.1 ± 6.18 SD), with water clarity at these localities ranging from 0.9 to 12 m. Calves represented 9.37% of all individuals sighted. Unconfirmed sightings suggest that the porpoise is present in the southern Gulf of California. Fishermen interviewed in San Felipe, Baja California Norte, were familiar with vaquita, and some have caught the porpoise in gillnets.

Manuscript accepted 23 January 1990.
Fishery Bulletin, U.S. 88:339–346.

The vaquita *Phocoena sinus* (Norris and McFarland 1958) is among the rarest and least understood of the Cetacea. In the 30 years following its initial description (Norris and McFarland 1958) very little new information about the porpoise had been obtained. Brownell (1986) reported that only 45 confirmed records of vaquita existed. These consisted of skulls and skeletons (Noble and Fraser 1971, Orr 1969) and about 20 reported sightings obtained between 1958 and 1986 (Norris and McFarland 1958, Norris and Prescott 1961, Villa-R. 1976, Wells et al. 1981). However, Brownell (1986) argued that only four of the sightings were valid.

Increased study of the porpoise in recent years has yielded new information through descriptions of recovered specimens (Magatagan et al. 1984, Brownell et al. 1987), reported sightings (Robles et al. 1986, Vidal et al. 1987, Silber 1988), and behavioral accounts (Silber et al. 1988). Norris and McFarland (1958) described the range of *P. sinus* as occurring in the upper Gulf of California and probably extending south along the Mexican coast, but Brownell (1986) maintained that the range was limited to the upper Gulf of California.

The vaquita population has been impacted by gillnetting activities and other forms of habitat degradation in recent decades (Brownell 1983, Barlow 1986). The species continues to experience mortality at an unknown rate in gillnets (Brownell 1983, Silber 1988) set primarily for totoaba *Totoaba macdonaldi* and various species of shark.

The objective for the initial year of the present study (1986) was to locate *P. sinus*, and subsequently (1987, 1988) to gather information on the ecology and distribution of the porpoise. Visual surveys were conducted from boat and aircraft in an attempt to determine the vaquita's distribution, range, and habitat utilization. Reported here are the results of three seasons of study on the vaquita conducted in the northern Gulf of California in the springs of 1986–88. I have also included a discussion of unconfirmed sightings in the southern Gulf that may reflect the historical range of *P. sinus*.

Materials and methods

Vessel surveys and sighting data

Boat surveys for *Phocoena sinus* were conducted in the northern Gulf of California using an 8-m Boston Whaler. A total of 1715 km of survey transects was conducted on 71 days during the three years (Figs. 1, 2a). The study was conducted in the spring months because (1) operational costs and logistic (e.g., boat time) restrictions limited field work duration, (2) conversations with fishermen in the upper Gulf in 1986 suggested that vaquita were most abundant (perhaps only present) in March–May, and (3) the number of sightings that we obtained (two porpoises in 485 km sur-

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

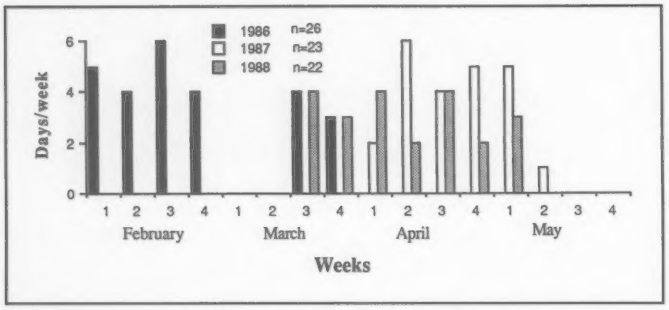

Figure 1
Number of days per week spent conducting transects and observations of *Phocoena sinus* in 1986, 1987, and 1988.

veyed) in February 1986 appeared to support information gathered from fishermen. For these reasons, the decision was made to concentrate survey efforts in March–May, when the likelihood of encountering the porpoise was believed greatest.

During vessel transects, two to four observers positioned 3.5 m above the water surface searched with unaided eyes and binoculars (7 and 10×) the area in front, and about 200–300 m on either side, of the vessel's track. Observers also regularly scanned to greater distances. During all surveys the vessel traveled consistently 10–11 km/hour. Transects conducted in 1986 were restricted primarily to nearshore areas. In subsequent field work inshore surveys were augmented by transects farther from shore.

For each porpoise sighting, the number of individuals seen was estimated and sighting locations were determined by triangulation from landmarks. Water depths were obtained with a JRC color video depth sounder or from a nautical chart. Water clarity (using a Secchi disc) and temperature were measured at most sighting locations. Sea states were obtained by visual estimate according to the Beaufort scale. No surveys were conducted when sea state exceeded Beaufort 3, and the majority were conducted in sea states of 1.

Aerial surveys

Limitations imposed by time, weather, and financial constraints prevented repeated vessel surveys south of lat. 30°30′. However, aircraft surveys were conducted as far south as lat. 29°34′N (Fig. 2b). A total of 1521 km was flown on three days, 3–5 May 1988, concentrating on the upper Gulf.

Fishermen interviews

Fishermen in San Felipe, Baja California Norte, and in the vicinity of La Paz, Baja California Sur, were interviewed in an attempt to obtain qualitative information with regard to the natural history, range, and distribution of the vaquita. Questions were asked regarding type of fishing, target species, years of employment, and location of fishing. The men were asked if they recognized vaquita after viewing photographs of living and dead *P. sinus* and other odontocetes common to the area. The interviews were intended as general informational surveys of local knowledge to direct future study of vaquita and preliminary assessments of fishing effort and vaquita entanglement rates. Information derived from interviews with fishermen has been presented, although questioning methodology and sample sizes were insufficiently rigorous to draw definitive conclusions with regard to vaquita distribution.

Results

Vaquita sightings

Vaquita were seen on 51 occasions, representing an estimated 96 individuals during boat and aircraft surveys (Table 1). A total of 43 porpoises was seen while conducting vessel transects, a sighting rate of 2.51 individuals/100 km surveyed. The remainder of the sightings occurred while tracking porpoises, collecting other types of data, or otherwise not engaged in visual transects. The paucity of sightings relative to the extent of the survey emphasized the rarity of the porpoise.

All sightings of vaquita occurred north of lat. 30°45′N, and all but two sightings (96.1%) occurred less than 40 km from San Felipe, Baja California Norte (Fig. 2a). Most sightings (94.2%) occurred in sea states 0 or 1 (Fig. 3). In 90.2% ($n = 46$) of all sightings, porpoises were observed in small groups (≤ 3 individuals). Mean group size was 1.9 ± 1.24 SD individuals per group (Table 1) and the group size mode was one (Fig. 4). For 86.3% ($n = 44$) of all porpoise sighting locations, water depths ranged from 21 to 35 m ($\bar{x}$ 25.7 ± 6.36 SD; overall range 13.5–37.0) (Fig. 5), and most sightings occurred 11 to 25 km from the nearest shore

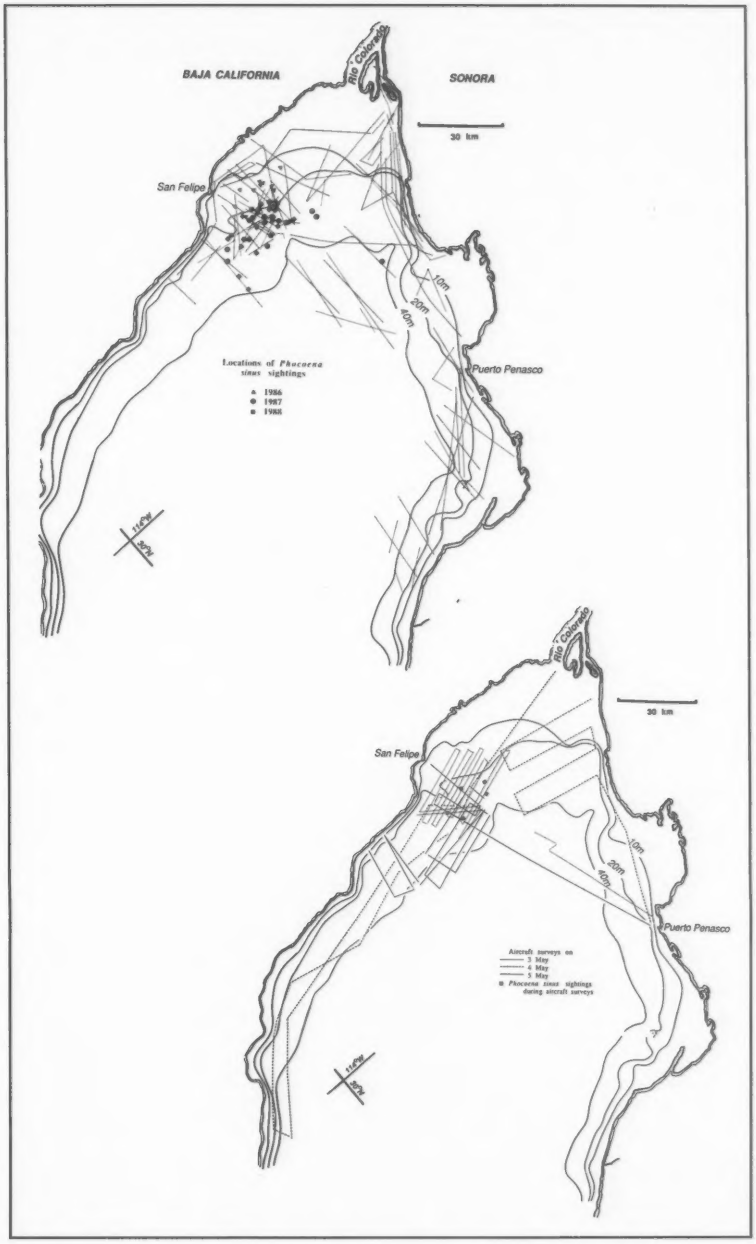

Figure 2
Phocoena sinus sightings and vessel transects conducted in 1986, 1987, and 1988 (top) and aircraft surveys on 3–5 May 1988 (bottom).

($\bar{x}$ 18.3±6.10 SD; range 2.4–32.2) (Fig. 6, Table 1). Water clarity at sighting locations ranged from 0.9 to 12 m. During four vaquita sightings the boat's depth sounder indicated concentrated layers at 15 (n = 2), 23, and 25 m, possibly representing schooling bait fish or squid upon which the porpoises may have been feeding. On numerous occasions, vaquita surfaced in or alongside surface slicks or long bands of flat water surrounded by rippled water.

Calves represented 9.37% of all individuals. One very young calf was observed on 9 April 1987. It was estimated at <2 days old because of its size, a dorsal fin

Table 1

Summary of all *Phocoena sinus* sightings in the northern Gulf of California, 1986–88. Group sizes are represented by mean, one standard deviation, and range.

Year and dates		Sightings	Distance to shore (km)	Depth (m)	Water temperature (°C)	Water clarity (m)
1986	*N*	16	16	16	12	12
2 Feb.–27 Mar.	$\bar{x}$	1.7	14.3	21.0	21.5	2.4
	SD	0.87	4.50	5.00	1.83	0.81
	Range	1–4	2.4–20.0	13.5–25.0	17.0–23.0	0.9–4.0
	Est. total ind.	27				
1987	*N*	22	22	22	12	13
8 Apr.–7 May	$\bar{x}$	2.1	19.3	27.5	22.9	8.2
	SD	1.57	5.71	4.73	2.09	2.46
	Range	1–7	15.3–32.2	20.0–37.0	21.0–26.0	5.0–12.0
	Est. total ind.	46				
1988	*N*	13	13	13	8	7
21 Mar.–5 May	$\bar{x}$	1.8	20.7	29.5	19.2	4.1
	SD	1.01	6.58	5.87	0.46	1.07
	Range	1–4	7.0–29.0	22.0–40.0	18.5–20.0	2.5–6.0
	Est. total ind.	23				
All years	*N*	51	51	51	32	32
	$\bar{x}$	1.9	18.3	25.7	21.5	5.0
	SD	1.24	6.10	6.36	2.23	3.10
	Range	1–7	2.4–32.2	13.5–40.0	17.0–26.0	0.9–12.0
	Est. total ind.	96				

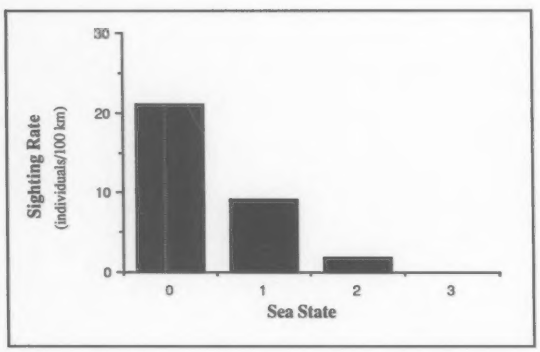

Figure 3
Phocoena sinus sighting rate (individuals/100 km) relative to sea state.

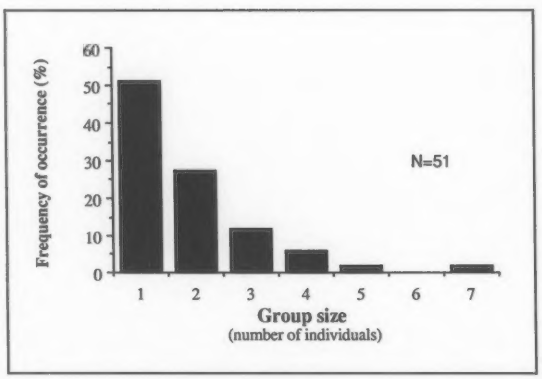

Figure 4
Phocoena sinus group size.

that was not yet fully erect, and the ungainly manner in which it lifted its head from the water with each surfacing.

Aerial surveys

Eleven *Phocoena sinus* (five sightings) were seen during aircraft surveys. All aerial sightings took place between San Felipe and Rocas Consag, and none occurred farther south along the Baja peninsula coast (Fig. 2b), although much less effort was dedicated to this area in relation to the extreme upper Gulf. The number of aircraft surveys was relatively small and non-random. Nonetheless, they served to support *P. sinus* distribution patterns observed during vessel surveys, failed to yield sightings south of the area surveyed by vessel, and illustrated the utility of aircraft as a platform of observation in future study and census of the species.

Sympatric vertebrates

Other marine vertebrates were seen near *P. sinus*;

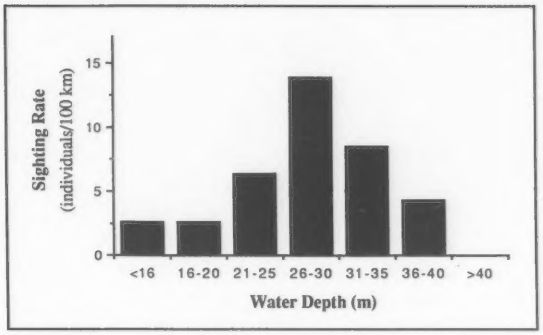

Figure 5
Phocoena sinus sighting rate (individuals/100 km) relative to water depth.

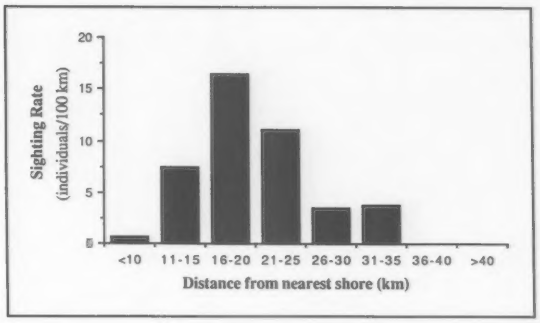

Figure 6
Phocoena sinus sighting rate (individuals/100 km) relative to distance from nearest shore.

affiliations that probably represent utilization of a similar habitat by two or more species rather than active association. Twice, Bryde's whales *Balaenoptera edeni* were seen <1 km from *P. sinus*, and three times common dolphins *Delphinus delphis* were observed <1.5 km from the porpoise. Numerous times black storm-petrels *Oceanodroma melania* and Bonaparte's gulls *Larus philadelphia* dipped into the wake of surfacing vaquita. Manta rays *Manta birostris* were seen once near porpoises.

In addition to vaquita, five other marine mammal species were common within the study area, including bottlenose dolphins *Tursiops truncatus*, common dolphins, fin whales *Balaenoptera physalus*, Bryde's whales, and California sea lions *Zalophus californianus*. There appeared to be a general segregation by location and water depth among the three most common odontocet species. The distribution of *P. sinus* overlapped that of *Delphinus* and *B. edeni*, but not that of *Tursiops* and *B. physalus* (Silber et al. In prep.). Bottlenose dolphins were consistently seen in more shallow water than were vaquita, and common dolphins were generally seen in greater, but comparable, water depths as vaquita. Data on sympatric marine mammals will be presented in greater detail elsewhere (Silber et al. In prep.).

Unconfirmed sightings and fishermen interviews

In February and April 1983 cetaceans that may have been *P. sinus* were seen near Cerralvo Island (24°10′N; 109°55′W) by a scientist who has extensive experience with marine mammals and Gulf of California fauna (G. Notarbartolo di Sciara, Piazza Duca d'Aosta 4, 20124 Milano, Italy, pers. commun., May 1984). In both sightings, the animals were 10–50 m from the observer. They were described as being small, possibly possessing a blunt rostral profile, and surfacing "unobtrusively" in small groups. They were "quite distinct from *Tursiops*, *Delphinus*, or *Lagenorhynchus*" (G. Notarbartolo di Sciara, pers. commun., May 1984). If true, these unconfirmed sightings occurred in an area >850 km south of our southernmost sightings, and extend the present known range considerably.

Based on these observations, the decision was made to interview fishermen in the southern Gulf about the presence of vaquita. In 1987, 17 fishermen from La Paz were interviewed about their fishing practices and their knowledge of the vaquita (Table 2). In most cases the fishermen had spent considerable time on the water (fishing 4–6 days/week, 3–12 months/year, for 5–51 years; $\bar{x} = 20.6$ yrs). Fishermen in the La Paz area generally had no knowledge of vaquita; however, one man was familiar with the porpoise and indicated that he had seen it several times near San Jose Island (25°00′N; 110°40′W), 80 km north of La Paz. Unlike others interviewed, this man was one of two who had been fishing for over 50 years and he had worked in an area (the coast near San Jose Island) different from the other fishermen. In addition, his knowledge of the natural history of marine mammals was regarded as being accurate by the interviewer (D. Aurioles, Centro de Investigaciones, Biologicas B.C.S., APO Postal 128, La Paz, Baja California Sur, México, pers. commun., June 1987). One fisherman described netting near San Jose Island a small cetacean that had rounded ("acorn-like") teeth, a feature characteristic of the genus *Phocoena*.

All fishermen interviewed in San Felipe ($n = 7$) expressed a knowledge of vaquita, and two said that they had entangled the porpoise while fishing for totoaba. Although taking totoaba is illegal, three men indicated that they continue to use gillnets for totoaba.

Table 2

Summary of interviews with fishermen in La Paz, Baja California Sur, and San Felipe, Baja California Norte, regarding fishing practices and knowledge of *Phocoena sinus*.

		San Felipe	La Paz
Number fishermen interviewed		7	17
Distance from home port (km)	$\bar{x}$	37.4	37.8
	SD	39.48	22.32
	Range	1–100	5–112
Number of years engaged in fishing	$\bar{x}$	17.8	23.4
	SD	12.50	15.51
	Range	6–35	5–51
Type of fishing		Gillnet, longline, hook-and-line	Longline, gillnet, trawl, diving
Target species		Shrimp (n = 6) Totoaba (n = 3) Shark (n = 2) Marlin (n = 1) Dorado (n = 1) Yellowtail jack (n = 1)	Spanish mackerel (n = 14) Shark (n = 9) Pacific manta (n = 1) Snapper (n = 1) Striped mullet (n = 1)
Fishing effort		12 mo/yr (n = 4) 3 mo/yr (n = 3)	12 mo/yr (n = 11) 10 mo/yr (n = 1) 3–6 mo/yr (n = 3)
Recognition of photos of *P. sinus*		Yes (n = 7)	Yes (n = 1); No (n = 16)
Estimated total porpoises killed		3–4	0
Common names used		Cochito, cochinito, and vaquita = *P. sinus*	Vaquita = *Kogia* or *Phocoena* spp. Duende = *Lagenorhynchus* Cochinito = *Delphinus* Cochito = *Globicephala*

The vernacular name for *P. sinus* tended to vary between communities and individuals. Fishermen in San Felipe referred to *P. sinus* as "cochito," "cochinito," and "vaquita." In contrast, for La Paz fishermen "vaquita" refers to *Kogia simus* or *Phocoena* spp., whereas "cochinito" refers to *Delphinus delphis*, "cochito" to *Globicephala macrorhynchus*, and "duende," also meaning *P. sinus* in some communities (Magatagan et al. 1984), refers to *Lagenorhynchus obliquidens* (D. Aurioles, pers. commun., June 1987).

Discussion

Although surveys were conducted throughout the upper Gulf, sightings of *Phocoena sinus* were limited almost entirely to the western side. One or a combination of the following features may account for vaquita distribution patterns in the upper Gulf. Relative to the eastern shore, the western boundary exhibits lower surface temperatures (Robinson 1973) resulting partly from northward-bearing upwelled water from the Midriff Island region. With respect to the eastern coastline of the upper Gulf, the western perimeter is characterized by stronger north-south tidal currents yearround (Hendrickson 1973) which may contribute to increased mixing on the west coast.

Vaquita often surfaced near surface slicks, which are caused by tidally induced internal waves (Ewing 1950, Shanks 1983) or areas of convergence of different water masses, a common feature of the northern Gulf of California (Hendrickson 1973, Lepley et al. 1975). Surfacing near slicks has been noted in other cetaceans, including *Feresa attenuata*, *Steno bredanensis*, and *Pseudorca crassidens* (K.S. Norris, Cent. Mar. Stud., Univ. Calif., Santa Cruz, CA 95064, pers. commun., Aug. 1987). Concentrations of small marine organisms are associated with internal waves (Shanks 1983, 1988; Kingsford and Choat 1986). Vaquita and other cetaceans may be drawn to aggregated prey in these features.

It is believed by some researchers that the entire *P. sinus* population is limited to the upper Gulf, which represents the smallest range of any marine cetacean (Brownell 1986, Barlow 1986); however, the actual range remains unsubstantiated. Although presently

untested, I suggest that vaquita occur in the upper Gulf year-round, and although the majority of the population may have receded to the upper Gulf following a relatively recent decline in population size, some individuals are probably scattered throughout the Gulf as separate subpopulations or a sparsely dispersed single population. Reported sightings of *P. sinus* outside the northern Gulf (Scammon 1874, Norris and McFarland 1958, Norris and Prescott 1961, Villa-R. 1976; presented here) suggest the possibility of a greater historical range. However, extensive field work on cetaceans near the Midriff Islands, Guaymas, and Kino Bay areas has not yielded sightings of vaquita (L. Ballance, Dep. Biol., Univ. Calif., Los Angeles, CA 90024, pers. commun., May 1989; L.T. Findley, Escuela de Ciencias Marítimas y Alimentarias, Instituto Tecnológico y de Estudios Superiores de Monterrey, Unidad Guaymas, A.P. 484, Guaymas, Sonora, 85400 México, pers. commun., Nov. 1985; B. Tershy, Dep. Biol., Cornell Univ., Ithaca, NY 14853, pers. commun., Sept. 1987). Most phocoenids are cold-temperate water animals (Gaskin 1982), with ranges restricted to <20°C. Northern Gulf of California surface water temperatures in the summer and fall can exceed 28°C (Hendrickson 1973, Robinson 1973). If the porpoise is limited to this region, it deviates remarkably from other phocoenids in its ability to tolerate seasonal water temperature fluctuations.

Management recommendations

Exposure of the depleted *P. sinus* population to current levels of human impact may result in the demise of the species. Habitat degradation and pesticide contamination of the northern Gulf may contribute to the decline of *P. sinus*. However, vaquita mortality in gillnets (Brownell 1983, Robles et al. 1986, Silber 1988) may represent the most direct threat to the population, and increased efforts to reduce porpoise entanglement is imperative. Nets set for totoaba probably account for the highest percentage of incidental porpoise deaths. The totoaba is an endangered species and cannot be legally caught, sold, or exported. Nonetheless, illegal fishing continues due to the inability to enforce restrictions. Additional study is needed to quantify incidental mortality rates and to explore possible modifications of fishing amounts, timing, and technique. Vaquita sightings occurred predominantly in discrete locations and water depths. If widespread fishing bans are not possible, emphasis should be placed on excluding fishing from these areas. However, because maximum catch of totaba also occurs in spring (Flanagan and Hendrickson 1976), there will be difficulty achieving compliance by fishermen. Rigorous sanctions on importation of totoaba bound for U.S. markets are required. Additional boat and aircraft census surveys should be conducted to determine the vaquita population size, and to enhance current knowledge of the ecology of the porpoise. Large areas of the northern Gulf have been recommended for consideration as a Marine Sanctuary (B. Villa-R., Inst. Biol., Univ. Nal. Autón. México, A.P. 70-153, México, D.F. 04510, pers. commun., Feb. 1986), and these plans should be endorsed. Mexican and U.S. scientists should engage in joint efforts to monitor changes in the vaquita population size. Action by Mexican and U.S. governments, fishing cooperatives, cetacean biologists, and resource management personnel is necessary to the preserve the species.

Acknowledgments

This study would not have been possible without important contributions by the following field assistants: T. Silber, M. Newcomer. G. Ellis, H. Pérez-Cortés, G. Barros, D. Breese, T. Jefferson, L. Torrez-M., A. Velazquez-R., and A. Robles. These people endured the rigors of field work and high expectations of a demanding captain. I extend thanks to K. Norris, B. Villa-R., and R. Wells who provided encouragement and advice. I am grateful to D. Aurioles and H. Pérez-Cortés for interviewing fishermen in La Paz and San Felipe, respectively, and for observations provided by G. Notarbartolo di Sciara. The project received financial support from the Nature Conservancy, the Center for Marine Conservation, and the American Cetacean Society (Los Angeles Chapter), and logistical support from the Center for the Study of Deserts and Oceans, Project Lighthawk, and West Coast Whale Research Foundation. The study was conducted under Scientific Research Permits 301856, 300422, and 400036 issued by the Secretaría de Pesca, México. The paper was improved by comments from K. Norris, B. Würsig, R. Wells, M. Newcomer, and T. Jefferson. This paper is dedicated to my wife Trish.

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Incidental Take of Marine Mammals in Foreign Fishery Activities Off the Northeast United States, 1977–88

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Abstract. – Fishery observers aboard foreign commercial fishing vessels collected information on the incidental catch of marine mammals in the Exclusive Economic Zone (EEZ) off the northeastern United States since March 1977. Observer coverage on foreign vessels was 25–35% during 1977–82, and increased to 58%, 86%, 95%, 98%, 100%, and 100%, respectively, in 1983–88. During 1981–88, observers have covered most joint-venture fishing operations. During 1977–88, observers reported 538 marine mammals captured incidental to direct and joint-venture fishing activities. Eight cetacean species and three unidentified baleen whales were caught, principally in the fisheries for Atlantic mackerel *Scomber scombrus*, and squid *Illex illecebrosus* and *Loligo pealei*. Pilot whales *Globicephala* spp. (297/538) and common dolphins *Delphinus delphis* (203/538) comprised 93% of the catch. Chi-square tests indicate that significant differences in diel rates of capture occurred between the two species. The number of *Globicephala* spp. captured at night (2000–0400 h) in the Atlantic mackerel fishery was significantly less ($\chi^2 = 8.28$, $P < 0.03$) than the number caught during day (0800–1600 h) or dawn/dusk (1600–2000 h, 0400–0800 h). The number of *D. delphis* captured during daylight in the *Loligo* squid fishery was significantly less ($\chi^2 = 44.48$, $P < 0.001$) than the number caught at night or dawn/dusk. A minke whale *B. acutorostrata* (released alive) and individuals of two endangered species, a humpback whale *Megaptera novaeangliae* (released alive) and a right whale *Eubalaena glacialis*, were also captured incidental to fishing activity. During December 1986–February 1988, observers collected whole, dead, non-endangered mammals for detailed shoreside examination. Trawl contents at the time of capture and subsequent analysis of mammal stomach contents suggest that *L. pealei* is a major component of the mid-shelf and shelf-edge diet of common dolphins and pilot whales. Further, pilot whales, considered principally as teuthophagous, were observed to selectively feed on mackerel while on the Continental Shelf.

Manuscript accepted 16 January 1990.
Fishery Bulletin, U.S. 88:347–360.

Marine mammal/fishery interactions in United States waters have received widespread attention in recent years (Bonner 1982, Fowler 1982, Lowry 1982, Loughlin et al. 1983, Loughlin and Nelson 1986). These interactions, generally involving commercial fisheries (Mate 1980), are of two types: (1) direct or operational, and (2) indirect or ecological (Lowry 1982).

In the shelf waters off the northeastern United States, marine mammal/commercial fishery interactions have been described only for fisheries occurring in nearshore waters (Gilbert and Wynne 1985). These interactions occur in the fixed-gear fisheries for American lobster *Homarus americanus*, the surface-gillnet fishery for Atlantic herring *Clupea harengus* and Atlantic mackerel *Scomber scombrus*, and the groundfish-gillnet fishery for assorted finfish, principally Gadidae and Pleuronectidae. Two principal marine mammals taken incidentally in these fisheries are the harbor porpoise *Phocoena phocoena* and the harbor seal *Phoca vitulina*. The gray seal *Halichoerus grypus* is infrequently captured. These three species are known to feed on fish caught in nets and to become entangled, thereby damaging fishing gear.

Marine mammal/fishery interactions in the deeper, offshore waters off the northeastern United States have not been previously documented. Under the provisions of the United States Marine Mammal Protection Act (MMPA) of 1972 a General Permit system was established by the National Marine Fisheries Service (NMFS) allowing incidental taking of marine mammals in commercial fishing operations. All domestic and foreign fishing vessels were required to have a valid permit on board that established an allowable limit on the number of non-endangered marine mammals that could be taken within a specified fishery (i.e., mackerel, squid). The Magnuson Fishery Conservation and Management Act of 1976 as amended in 1983, (MFCMA, Public Law 94-265) mandated the placement of Fisheries Compliance Inspectors, or observers,

beginning in 1984, on 100% of all foreign fishing vessels operating within the 200-mile outershelf and slope waters off the United States. (This area is further referred to as the Exclusive Economic Zone, or EEZ). Since that time in 1984, reporting of marine mammal takes incidental to foreign fishing activities has been more effectively monitored by species and fishery.

In this paper we summarize the observed incidental take of marine mammals from all foreign fishing activities that operated within the EEZ off the northeastern United States from 1977 to 1988. The incidental take of common dolphins *Delphinus delphis* and of pilot whales *Globicephala* spp.*, the two most frequently caught species, are examined relative to the type of fishery in which they were taken, the nationality involved in the fishery operation, and the time of the incidental take (day versus night). Morphological measurements, sex, and stomach contents for 33 of the common dolphins taken during 1986 and 1988 are also reported in this study. These measurements and records are the first such information taken from any marine mammal specimens recently killed in the waters off the northeastern United States.

Summary of foreign fisheries

Fishing operations

Large-scale foreign fishing activity began off the U.S. east coast in the early 1960s with the arrival of the distant-water fleet (DWF) from Europe and Japan. Initially, the DWF harvested groundfish (Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, hakes, flounders, etc.) and pelagics (Atlantic herring and Atlantic mackerel) (Brown and Halliday 1983). Declining fish stocks, coupled with management measures implemented in the late 1960s, under the auspices of the International Commission for the Northwest Atlantic Fisheries, resulted in the DWF shifting emphasis to "under-utilized" species, such as long-finned squid *Loligo pealei*, short-finned squid *Illex illecebrosus*, and Atlantic butterfish *Peprilus triacanthus*.

The MFCMA, which became effective March 1977, significantly altered DWF activities within the EEZ. Fishing effort was immediately reduced, and the number of foreign vessels operating within the east coast EEZ declined from a high of 161 vessels in 1977 to 26 in 1988. From 1977 through 1982, an average of 120 different foreign vessels per year (range 102–161) operated within the EEZ. In 1982, there were 112 different foreign vessels; 16%, or 18, were Japanese tuna longline vessels operating off the east coast. The Northeast Region Observer Program assumed responsibility for observer coverage of the east coast Japanese tuna longline fishery in 1982. This fishery has been conducted from the Canadian boundary-line south to Florida and, prior to 1982, in the Gulf of Mexico. In 1983, a decrease in the total allowable catch allocated to each foreign country fishing off the east coast resulted in fewer foreign vessels operating within the EEZ. Between 1983 and 1988, the numbers of foreign vessels operating within the EEZ each year were 67, 52, 62, 33, 27, and 26, respectively. Observer coverage (the ratio of observer coverage days to the number of foreign fishing days) ranged from 25 to 35% for the period 1977–82. Coverage increased steadily since 1982, and was maintained at 58%, 86%, 95%, 98%, 100%, and 100% in 1983-1988, respectively.

Since 1977, fourteen nations have been given catch allocations to operate off the east coast within the EEZ. Direct fishing (DWF catching and processing their own catches) was limited to five Outer Continental Shelf locations referred to as fishery windows (Fig. 1) and to specified times of year. From 1977–83, the DWF led by Italy, Spain, and Japan principally targeted long-finned and short-finned squid within these windows. Direct squid fishing operations ceased at the end of the 1986 fishing season.

Joint-venture fishing operations (U.S. captains transfer their catches to foreign processing vessels) began in 1981. Squid joint ventures, which were unrestricted areally, were authorized without any associated direct fishing allocations. In 1983 the German Democratic Republic (GDR), and in 1984 the Netherlands, commenced joint-venture operations for Atlantic mackerel off the east coast. Mackerel joint ventures which have been authorized with associated allocations for direct fishing have not been restricted to the fishery windows. In 1988, Poland also commenced commercial fishing operations for Atlantic mackerel that included joint-venture and direct fishing. Prior to 1988, Poland conducted a research fishery each year between 1981 and 1987 for Atlantic mackerel that involved Polish catching/processing vessels staffed with Polish and U.S. fishery data collectors.

Foreign vessels engaged in *Loligo* and *Illex* squid fishing operations used off-bottom trawls, and did not utilize squid attracting devices, such as lights, during night-time fishing. In the Atlantic mackerel fishery, both off-bottom high-opening trawls and pelagic trawls

*The distribution of the Atlantic pilot whale *Globicephala melaena*, the northern species, overlaps with the short-finned pilot whale *G. macrorhyncha*, mainly a southern species, between about 35°30'N to 38°00'N (Leatherwood et al. 1976). Although, *G. melaena* is the most common and the most likely taken in the DWF foreign fisheries, there is a possibility that the southern species might also be occasionally taken. Therefore, in this paper both pilot whales are considered together.

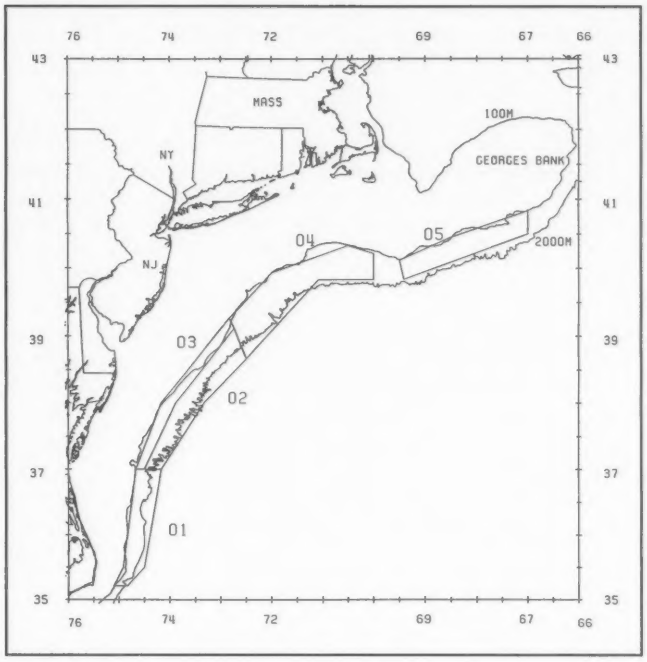

Figure 1
Foreign fishery windows within the EEZ off the northeastern United States.

have been used; currently the DWF utilizes several different pelagic trawls.

Principal target species

Loligo or long-finned squid

Although *Loligo* occurs from the Gulf of Mexico north to New Brunswick, Canada (Summers 1967), the distribution of long-finned squid (hereafter referred to as *Loligo*) is primarily from Cape Hatteras, North Carolina, to Georges Bank and into the Gulf of Maine (Lange 1980). *Loligo* overwinters along the shelf edge from Cape Hatteras to Georges Bank at water temperatures generally >8°C (Lange and Sissenwine 1980). During spring and summer *Loligo* moves into nearshore waters to spawn (Summers 1967). Commercial concentrations are found primarily off southern New England and the mid-Atlantic regions from about Georges Bank to Baltimore Canyon (Lange 1980, Lange and Johnson 1981). DWF fishing prior to the MFCMA occurred at depths of 100–500 m along the shelf edge from November through March (Lange 1980), but since 1977 fishing operations have been restricted in area and season. Since 1987, the allocation for *Loligo* has been reduced strictly to bycatch in the Atlantic mackerel fishery; therefore, DWF *Loligo* fishing has been suspended.

Illex or short-finned squid

The short-finned squid (hereafter referred to as *Illex*) is a more northern species than *Loligo*, ranging from Florida to Newfoundland (Squires 1957). In late autumn (October–December), *Illex* moves offshore toward the shelf edge and beyond (Lange and Sissenwine 1980). Spawning is believed to occur offshore at great depths, primarily from December to March (Lange and Sissenwine 1980). During warmer months *Illex* move nearshore to feed (Lange 1980). Commercial concentrations occur from the mid-Atlantic, near Baltimore Canyon, to Newfoundland (Lange and Johnson 1981). The DWF *Illex* fishery took place from June through October, while this species is on the shelf (Lange 1980). In 1987, *Illex* allocations for DWF fisheries were suspended. At present, there is no direct foreign fishing effort for this species.

Atlantic mackerel

Atlantic mackerel, a major target species of the DWF, overwinter along the edge of the continental shelf between Cape Hatteras and Sable Island, Nova Scotia (Anderson and Paciorkowski 1980). The overwintering population consists of two components (southern and northern), which separate in spring. The southern component moves nearshore in early spring along the

Virginia Capes and proceeds northeastward to spawn off the New Jersey and Long Island coasts from mid-April to early May. By midsummer, the southern component reaches the Gulf of Maine where it remains throughout summer (Anderson and Paciorkowski 1980). Migration out of the Gulf of Maine begins in autumn as the southern component returns to deeper, offshore waters. The northern component migrates further north in spring along the Nova Scotian shelf to the Gulf of St. Lawrence where spawning occurs during June–July (Anderson and Paciorkowski 1980). The northern component begins leaving the Gulf of St. Lawrence in September and returns to the mid-Atlantic region to overwinter.

The seasonal DWF mackerel fishery occurs in the mid-Atlantic region during the winter when both components of the mackerel population concentrate primarily along the shelf edge (Anderson and Paciorkowski 1980), although commercial quantities are sometimes encountered in waters as shallow as 30 m.

Methods and materials

Data collection on incidental take

Observers monitor compliance with applicable fishing regulations, collect biological data and samples, and serve in a liaison role, when needed, between foreign and domestic captains. In the northeast region, observer training is the responsibility of the NMFS Observer Program. Between 1977 and 1985, observers routinely recorded the number of marine mammals taken incidentally in foreign fishing activities. In 1986, a new sampling protocol was implemented to collect additional information on marine mammals, sea turtles, and marine debris. Observers are now required to complete sighting forms, document the circumstances of capture and obtain biological data on incidentally captured marine mammals* and sea turtles. Marine mammal biological sampling includes five straight-line body measurements (e.g., snout to fluke notch, flipper length, flipper width, fluke width, and dorsal fin height), girth at pectorals, sex, and total weight. Additionally, when feasible, incidentally caught marine mammals are frozen whole, brought ashore, and later examined by researchers at the Smithsonian Institution.

Data analysis on incidental take

A paired Mann-Whitney test (Zar 1974) was used to test for differences between the total number of cetaceans killed per day (kill-rate) in the 1984–88 Netherlands and the GDR mackerel fishery. Data for Poland were not included, because that country did not begin commercial fishing until 1988. Because a Mann-Whitney test examines only differences in paired data sets, a Friedman rank sums test (Hollander and Wolfe 1973) was used to examine the kill-rates between Italy, Spain, and Japan in the 1984–86 *Loligo* squid fishery.

Randomly selected samples of 334 trawl logs from the 1985 Atlantic mackerel fishery (from Netherlands) and 1018 trawl logs from the 1985 *Loligo* squid fishery (from Italy) were used to determine the expected level of fishing effort (number of tows) for each of three time periods—Day (0800–1600), Dawn/Dusk (0400–0800 and 1600–2000), and Night (2000–0400)—within each fishery. The Chi-Square Statistic was then used to determine whether there were significant differences in the numbers of common dolphins and pilot whales incidentally taken in each fishery (relative to fishing effort) due to time of day of the take.

Data analysis on stomach contents, sex and total length

A total of 95 common dolphins and 169 pilot whales taken between 1986 and 1988 were measured (total standard length) and sexed at sea. Stomach contents from 33 of the common dolphins were examined by Smithsonian Institution personnel, and the information was provided for this paper. Prior to 1986, stomach contents and sex data were not collected.

Results

Observers reported 538 marine mammals incidentally caught during foreign fishing activities in the EEZ off the northeast United States between March 1977 and December 1988 (Table 1). Pilot whales were the most frequently caught marine mammal with 297 caught, representing 55% of the total marine mammal take between 1977 and 1988 (Table 1). Common dolphins were the next most-frequently-taken cetacean with 203 caught, composing 38% of the total incidental takes. Approximately 5% of the total catch consisted of three other members of the Delphinidae: Atlantic white-sided dolphin *Lagenorhychus acutus*, bottlenose dolphin *Tursiops truncatus*, and Risso's dolphin *Grampus griseus* (Table 1).

Six large whales were reported caught or entangled during fishing operations. One subadult or juvenile right whale *Eubalaena glacialis* (based on observer identification and estimated length of 6 m) and one unidentified baleen whale were taken in the *Loligo* fishery. A humpback *Megaptera novaeangliae*, minke

*In this paper, an incidental take is defined as any live marine mammal or any carcass caught during foreign fishing activity.

Table 1

Summary of incidental take of marine mammals as reported by U.S. fisheries observers on foreign vessels in the shelf and slope waters of the northeastern United States. Values in parantheses represent animals released alive. (jv = joint venture)

Year/ Fishery	Country	Common dolphin	Pilot whale	White-sided dolphin	Bottlenose dolphin	Risso's dolphin	Unid. dolphin	Right whale	Humpback whale	Minke whale	Unid. whale	Total
1977–83												
Illex	Italy		1				2					3
	Japan		1									1
	Mexico		1									1
	Spain		3									3
	USA (jv)		6									6
Loligo	Italy	2	2									4
	Japan	1	3				1					5
	Mexico				1							1
	Spain	1	5					1			1(1)	8(1)
Tuna	Japan		2				1		1(1)		1	5(1)
Hake	USSR		2		1						1	4
Mackerel	Poland	4	13		1							18
Totals		8	39		3		4	1	1(1)		3(1)	59(2)
1984												
Illex	USA (jv)		1									1
Loligo	Italy	3	3	2								8
	Spain		7									7
Tuna	Japan					1						1
Mackerel	GDR		1									1
	Netherlands		11									11
	Poland				1							1
Totals		3	23	2	1	1						30
1985												
Loligo	Italy	56	1			1						58
	Japan	1										1
	Spain	4	4				1					9
Mackerel	GDR		8	3								11
	Netherlands	5	32		3							40
	Poland		1									1
	USA (jv)		1									1
Totals		66	47	3	3	1	1					121
1986												
Loligo	Italy	54	1			1						56
	Spain	1										1
	USA (jv)		2									2
Tuna	Japan									1(1)		1(1)
Mackerel	GDR	4	12(1)									16(1)
	Poland	3	1(1)									4(1)
	USA (jv)	14	4									18
Totals		76	20(2)			1				1(1)		98(3)
1987*												
Illex	Italy					1						1
Mackerel	GDR	11	12(1)									23(1)
	Netherlands	7	11									18
	USA (jv)	1	3									4
Totals		19	26(1)			1						46(1)
1988												
Mackerel	GDR	20	27									47
	Netherlands		50	4	1							55
	Poland	11	58(3)	4	1		1					75(3)
	USA (jv)		7									7
Totals		31	142(3)	8	2		1					184(3)
1977–88 Totals		203	297(6)	13	9	4	6	1	1(1)	1(1)	3(1)	538(10)

*Directed foreign *Loligo* fishing operations ceased in 1986.

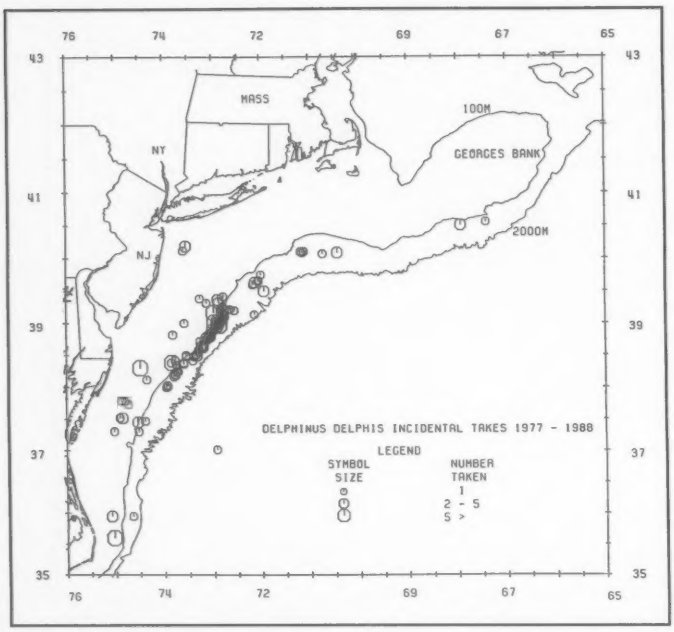

Figure 2
Distribution of incidental takes of common dolphin in foreign fishing activities off the northeastern United States, 1977–88.

Balaenoptera acutorostrata, and an unidentified baleen whale were also reported taken in the tuna longline fishery (Table 1). Another unidentified baleen whale was taken in the hake fishery.

Location of incidental takes of common dolphins and pilot whales

A total of 68% (n = 136) of the common dolphins captured in foreign fishing activities were caught along the shelf edge, represented by the 100-m isobath, between 37°30′N and 40°00′N latitudes (Fig. 2), and 69% (n = 138) of the common dolphins were taken between December and February. Most (n = 152) of the pilot whales captured during foreign fishing activities also occurred along the shelf edge (Fig. 3), and 83% (n = 246) were captured between March and July. Of the total number of pilot whales taken incidentally to fishing, 8% (n = 24) were captured between December and February, as compared with 69% for common dolphins.

Incidental takes by fishery and country

During 1977–83, 54% (32/59) of the incidental bycatch of marine mammals in foreign fishing activities was taken in the *Loligo* and *Illex* fisheries (Table 1). This high percentage is consistent with the distribution of DWF fishing effort during this period. Since 100% observer coverage of most fisheries did not begin until 1984, the number of marine mammals taken during this period is probably under-represented.

***Loligo* and *Illex* fisheries** A total of 61% (n = 123) of the total number of common dolphins taken during 1977–88 (n = 203) were caught in the *Loligo* fishery, and 94% (n = 116/123) of these takes occurred during 1985–86. Again, takes prior to 1984 were probably under-represented. Italian vessels caught 93% of the common dolphins taken in the *Loligo* fishery.

The total number of pilot whales caught in the *Loligo* fishery (n = 28) was 9.4% of the total number of pilot whales taken incidentally to all foreign fishing activities. Of the pilot whales taken in the *Loligo* fishery between 1984–86, 61% (n = 11/18) were taken by Spain.

No common dolphins were taken in the *Illex* fishery; however, 13 pilot whales were taken between 1977 and 1984. Of the pilot whales taken, 46% (n = 6) were caught by U.S. joint-venture vessels.

Atlantic mackerel fishery During 1984–88, 76 common dolphins were taken in the fishery for Atlantic mackerel (Table 1). Of the common dolphins taken in this fishery, 46% (n = 35/76) were caught by GDR vessels, 19% (n = 15) by U.S. joint-venture vessels, 18% (n = 14) by Polish vessels, and 17% (n = 12) by Dutch vessels.

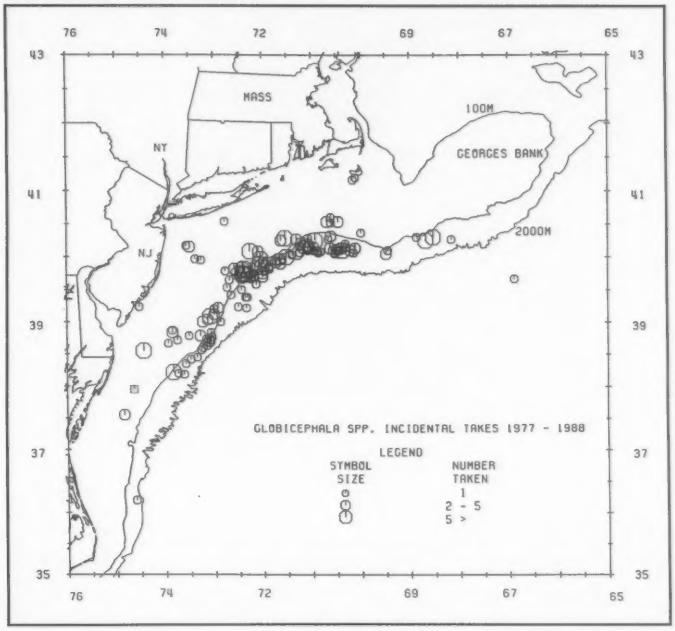

Figure 3
Distribution of incidental takes of pilot whales in foreign fishing activities off the northeastern United States, 1977–88.

Of the DWF fisheries mortality of pilot whales since 1984, 93% occurred in the Atlantic mackerel fishery (Table 1). During 1984–87, the Netherlands and the GDR caught 54 and 33 animals, respectively, which combined represent 90% ($n = 97$) of the pilot whales taken in the mackerel fishery during that 4-year period. In 1988, Poland began commercial fishing for Atlantic mackerel and caught 41% ($n = 58$) of the pilot whales taken that year. Although the Netherlands did not fish in the EEZ during 1986, they still caught 44% (104/239) of the pilot whales taken since 1984 in the Atlantic mackerel fishery.

Summary of kill rates by fishery and country

***Loligo* fishery** The total number of marine mammals (all species) killed per days fished (k/d rate) by Italy in the directed *Loligo* fishery was more than six times that of either Japan or Spain between 1984 and 1986 (period of nearly 100% observer coverage) (Table 2). During the years 1985 and 1986, this rate was approximately 10 times greater than the same rate for Spain, in spite of comparable number of days fished (Table 2). The k/d rates for 1984–86 between the three countries, however, are not significantly different using the Friedman test ($P<0.19$).

Atlantic mackerel fishery The k/d rate in the Atlantic mackerel fishery has varied both over years and among countries (Table 3). Between 1984 and 1988, the average kill rate for the GDR and the Netherlands was 0.12 k/d. The Netherlands annual k/d rates were 4 to 17 times greater than GDR rates, and differences in the k/d rates between these two countries are significant, $P<0.06$. With the inclusion of the 1988 takes by Poland, the all-years (pooled) k/d rate increases to 0.14 (Table 3). The 1988 k/d rates for each country were the highest observed during the 5-year period, 1984–88 (Table 3).

Summary of incidental take by fishery and time of day

***Loligo* fishery** The incidental take of common dolphins during daylight hours (0800–1600) was significantly less ($\chi^2 = 44.48$, 2 df, $P<0.001$) than the number captured during dawn/dusk or the night (Table 4). The number of pilot whales captured in the *Loligo* fishery did differ significantly by time period ($\chi^2 = 1.02$, 2 df) (Table 4).

Atlantic mackerel fishery Similar to the *Loligo* fishery, the number of common dolphins captured during daytime hours was significantly less ($\chi^2 = 20.42$, 2 df, $P<0.001$) than the number caught in tows at other time periods throughout the day (Table 5). The number of pilot whales caught in tows conducted during the night (2000–0400) was significantly less ($\chi^2 = 8.28$, 2 df,

Table 2

Numbers of cetaceans killed and days fished by Italy, Japan, and Spain while *Loligo* squid fishing off the northeastern United States, 1984–86. Numbers do not include animals captured and released alive.

	1984			1985			1986			Total		
	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d
Italy	1000	8	0.01	631	58	0.09	524	56	0.11	2155	122	0.06
Japan	267	0	0	73	1	0.01	26	0	0	366	1	<0.01
Spain	678	7	0.01	936	9	0.01	511	1	<0.01	2125	17	0.01
Total	1945	15	0.01	1640	68	0.04	1061	57	0.05	4646	140	0.03

Table 3

Numbers of cetaceans killed and days fished by German Democratic Republic (GDR), Poland, and Netherlands while Atlantic mackerel fishing off the northeastern United States, 1984–88. Numbers do not include animals captured and released alive.

	1984			1985			1986			1987			1988			Total		
	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d	days	kill	k/d
GDR	166	1	0.01	213	11	0.05	306	15	0.05	415	22	0.05	344	47	0.14	1444	96	0.07
Poland*	—	—	—	—	—	—	—	—	—	—	—	—	306	72	0.24	306	72	0.24
Netherlands	65	11	0.17	131	40	0.31	0	0	0	94	18	0.19	95	55	0.58	385	124	0.32
Total	231	12	0.05	344	51	0.15	306	15	0.05	509	41	0.08	745	173	0.23	2135	292	0.14

*Does not include scientific research.

Table 4

Observed and expected catch by time of day of common dolphins and pilot whales taken in the 1977–86 *Loligo* squid fishery off the northeastern United States.

Time of day*	Observed frequency	Expected frequency	χ^2
Common dolphins			
0800–1600	11	46	26.63
2000–0400	57	35	13.83
0400–0800			
1600–2000	55	42	4.02
$\chi^2 = 44.48$, 2 df			
$P<0.001$			
Pilot whales			
0800–1600	11	9	0.444
2000–0400	5	7	0.571
0400–0800			
1600–2000	9	9	0.000
$\chi^2 = 1.015$, 2 df			
$P<0.6017$, ns			

*Day (0800–1600), night (2000–0400), dawn/dusk (0400–0800, 1600–2000).

Table 5

Observed and expected catch by time of day of common dolphins and pilot whales taken in the 1984–88 Atlantic mackerel fishery off the northeastern United States.

Time of day*	Observed frequency	Expected frequency	χ^2
Common dolphins			
0800–1600	7	25.7	13.610
2000–0400	36	25.7	4.130
0400–0800			
1600–2000	34	25.7	2.680
$\chi^2 = 20.42$, 2 df			
$P<0.001$			
Pilot whales			
0800–1600	91	80	1.510
2000–0400	59	80	5.510
0400–0800			
1600–2000	90	80	1.250
$\chi^2 = 8.28$, 2 df			
$P<0.03$			

*Day (0800–1600), night (2000–0400), dawn/dusk (0400–0800, 1600–2000).

Table 6

Summary of stomach contents of 33 common dolphins killed in foreign fishing activities off the northeastern United States, 1986–88.

TL (cm)	Sex	Stomach content		Fishery
		Weight (kg)	Description	
195	M	1.17	Partial digested squid, few fish bones	Squid
205	M	0.48	Partly digested squid pens and beaks, a few hake otoliths	Squid
194	M	0.27	~50 cc squid beaks and pens, no fish remains	Squid
226	M	3.38	Mostly whole squid and some well-digested fish	Squid
205	M	0.89	1 L digested fish and 8–11 pairs of squid beaks	Squid
180	F	0.19	Squid	Squid
208	M	No data	No data	Squid
190	M	0.99	Squid	Squid
207	M	0.28	Squid	Squid
210	F	Empty		Squid
193	M	2.68	4 intact mackerel, a few squid beaks and pens, and two unknown fish	Mackerel
188	M	0.16	Few fish vertebrae and squid pens and beaks	Mackerel
209	M	2.20	No data	Mackerel
199	M	1.99	3 partially digested mackerel, squid beaks and pens	Mackerel
193	M	0.91	3/4 L fish bones, few small squid beaks	Mackerel
200	M	1.18	1 intact mackerel, 1 partly digested mackerel, no squid parts	Mackerel
202	M	No data	3/4 L fish including 3 whole mackerel and 2 pairs of squid beaks	Mackerel
196	M	2.15	6–7 intact mackerel and some squid beaks	Mackerel
200	M	1.90	1.5 L partially digested fish and 3 pairs of squid beaks	Mackerel
194	F	2.8	6 mackerel, 4 whole squid	Mackerel
188	F	1.34	Mackerel in fore stomach, squid pen in pyloric	Mackerel
203	M	1.81	3 mackerel (33 cm SL) and 2–3 well-digested mackerel	Mackerel
207	M	1.94	Mackerel	Mackerel
208	M	1.34	Mackerel	Mackerel
223	M	4.2	16 mackerel (30 cm SL) in main stomach, trace squid in pyloric	Mackerel
190	F	0.15	Trace squid	Mackerel
198	F	1.86	Squid and 1 mackerel (30 cm)	Mackerel
214	M	3.83	14 mackerel (25–38 cm SL)	Mackerel
216	M	1.21	Mackerel	Mackerel
205	M	3.04	Mackerel	Mackerel
216	M	3.86	7 mackerel (35 cm), and equal volume of digested mackerel	Mackerel
195	F	1.87	No data	Mackerel
204	F	1.99	Mackerel in fore stomach	Mackerel

$P<0.03$) than the number of pilot whales caught during the day or dawn/dusk (Table 5).

Food habits and morphometrics based on examination of animals collected in DWF fisheries

Food habits Stomach contents of 17 common dolphins taken in the mackerel fishery and 10 taken in the *Loligo* fishery reflected the target species of the respective fisheries (Table 6). Nine of the stomachs examined from dolphins taken in the Atlantic mackerel fishery contained only Atlantic mackerel. Eleven of the stomachs contained mixed fish (Atlantic mackerel and/or unidentifiable parts) and squid. One of the stomachs contained only squid. Data were not recorded for two stomachs. Examination of two stomachs taken from pilot whales caught in the Atlantic mackerel fishery contained only Atlantic mackerel.

In comparison, 4 of the 10 stomachs examined from dolphins taken in the *Loligo* fishery contained only unidentifiable squid parts. Four other stomachs contained squid spp. and unidentifiable fish parts. One stomach was empty and data were not reported for one stomach.

Morphometrics The sex ratio of the 95 common dolphins measured at sea during 1986–88 was 52 males, 22 females, and 21 not determined (70.3% male). These animals ranged in size from 150 to 290 cm (Fig. 4). The size range for males was 150–290 cm ($\bar{x}$ 209 cm), 185–260 cm ($\bar{x}$ 202 cm) for females. Of the dolphins measured, 33 were <200 cm in length. This places them in the prepubescent length-category provided by Collett and Saint-Girons (1984).

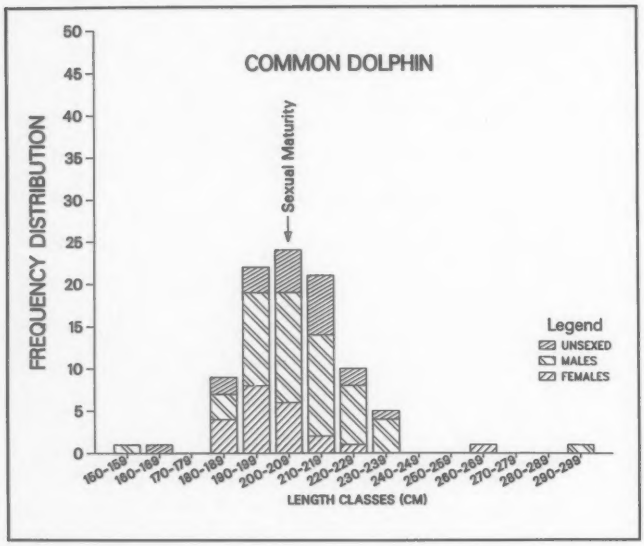

Figure 4
Length distribution of incidentally captured common dolphins measured by observers aboard foreign fishing vessels off the northeastern United States, 1986–88. Size at attainment of sexual maturity is from Perrin and Reilly (1984).

A total of 169 pilot whales measured during 1986–88 included 104 females, 40 males, and 25 not determined (72.2% female). These animals ranged in size from 199 to 510 cm (Fig. 5). Of the females, 85% ($n = 88$) measured 366–510 cm ($\bar{x}$ 429 cm), which is greater than the average length at attainment of sexual maturity (365 cm) as reported for *G. melaena* in the western North Atlantic by Perrin and Reilly (1984). The size range for the males was 199–470 cm ($\bar{x}$ 325 cm). No males recorded by observers reached the average length at attainment of sexual maturity (490 cm) reported by Perrin and Reilly (1984).

Discussion

Distribution of common dolphins and pilot whales relative to timing and location of take

The location (Figs. 2, 3) and timing of the incidental take (midwinter to late spring) of these two species are directly related to the seasonal distribution of each species. From mid-January to May, the distribution of common dolphins generally extends from Cape Hatteras northeastward to Georges Bank in mid- to outershelf waters (Hain et al. 1981, CETAP 1982, Payne et al. 1984). During mid- to late summer, many common dolphins move northward out of the EEZ onto the Scotian Shelf (Sergeant 1958, Sergeant and Fisher 1957) before returning southward to Georges Bank during late fall and winter. Therefore, the distribution of this species is most restricted during midwinter and early spring in the mid-Atlantic, coincident to the DWF *Loligo* and Atlantic mackerel fisheries.

Likewise, pilot whales are also distributed along the outershelf of the mid-Atlantic and southern New England waters of the EEZ during midwinter and spring (December–May). Throughout spring and early summer, pilot whales move northward along the shelf-edge and by summer–late fall their distribution is most widespread throughout the EEZ (CETAP 1982, Payne et al. 1984). Pilot whales were taken when their distribution was most concentrated along the southern New England shelf-edge in spring.

Incidental take by fishery and country

A large percentage of common dolphins were taken by Italy during *Loligo* squid fishing operations. This occurred despite reduction of Italian allocation and effort (i.e., days fished) in the *Loligo* fishery during 1985 and 1986. The Netherlands took a large percentage of pilot whales in the 1984–88 Atlantic mackerel fishery despite fewer days on grounds than GDR vessels. These takes appear to be more related to differences in fishing strategies (i.e., gear configuration, trawling and haulback speeds) than total effort. Currently there is insufficient information to evaluate the effect of different fishing techniques between countries on the total take or the k/d rates. Increased observer coverage and documentation of fishing activities should be helpful in evaluating and developing recommendations for modifying current fishing practices, resulting in a reduction of incidental marine mammal mortality.

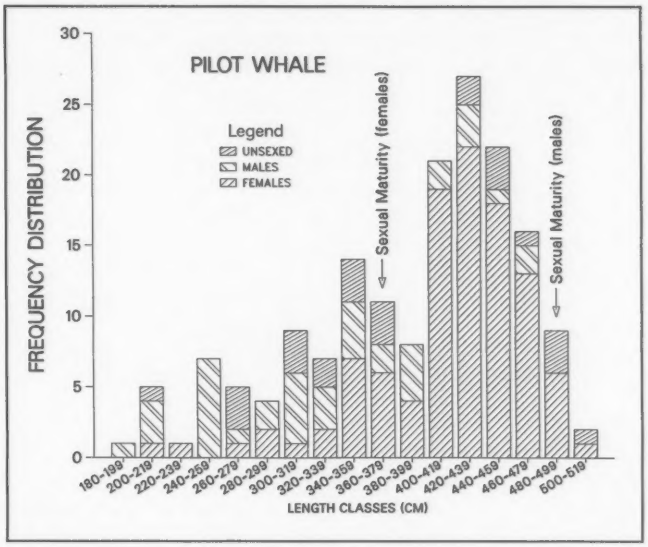

Figure 5
Length distribution of incidentally captured pilot whales measured by observers aboard foreign fishing vessels off the northeastern United States, 1986–88. Size at attainment of sexual maturity is from Perrin and Reilly (1984).

Incidental take of common dolphins and pilot whales relative to time of day and fishery

Significantly more common dolphins were captured during the *Loligo* fishery at night than during other time periods throughout the day. Possibly the diurnal movement upward at night would concentrate *Loligo* nearer the surface, thereby also concentrating common dolphins feeding on this prey. This would result in an increased likelihood of common dolphins capture due to a narrowing of the fishing area within the water column.

If common dolphins follow squids downward during daylight hours, then this would account for the lack of surface-feeding observations during the daytime. Conversely, if common dolphins feed principally at night, then common dolphins might become spatially separated from squid during daylight hours, resulting in a decreased likelihood of incidental capture. Although the reasons that common dolphins are caught at night in the DWF *Loligo* fishery are not readily apparent, it does seem that the day/night differences in capture are also related to a behavioral phenomenon of the dolphins, and not simply fishing practices.

Conversely, the take of pilot whales was significantly greater during daylight hours. Pilot whales were observed on numerous occasions in active pursuit and opportunistically feeding in and around the mouth of the net during haulback operations. Similar observations have been reported for the Pacific bottlenose dolphin and other species in Leatherwood (1975). The large size and widespread opening of pelagic mackerel trawls might serve to corral larger delphinid species such as pilot whales. Current data do not allow conclusive determination of whether the high incidence of pilot whale mortality during daylight hours is behavioral or the result of fishing practices by the Netherlands, GDR, and Poland.

Food habits

Common dolphins have been reported to feed on a wide variety of epipelagic and mesopelagic schooling finfishes and squids (Collett et al. 1981, Fiscus 1982, Fiscus and Niggol 1965, Fitch and Brownell 1968, Jones 1981, Nishiwaki 1972, Norris and Prescott 1961, Major 1986). Prey items collected from stomachs of common dolphins captured in the DWF indicate that *Loligo* and Atlantic mackerel are important prey items for dolphins during midwinter in the shelf waters of the mid-Atlantic.

Information on the dietary habits of pilot whales is limited, but they are considered teuthophagous, feeding principally on squid with fish as an alternative. Atlantic cod and Greenland turbot *Reinhardtius hippoglossoides*, which were taken off Newfoundland by overwintering pilot whales when squid were not available, are the only finfish prey items reported from the northwest Atlantic (Sergeant 1962, Mercer 1975).

We have not examined any stomachs of pilot whales taken in the DWF squid fisheries. However, it seems likely, based on qualitative examination of the relative abundance and co-occurrence of pilot whales and *Loligo* and known preferences for squid from the literature,

that *Loligo* is a principal prey item of pilot whales in the shelf waters of the mid-Atlantic during late winter and early spring. It also seems apparent that Atlantic mackerel could be considered an important prey of pilot whales in the mid-Atlantic. This conclusion is based on the observations of pilot whales feeding around and in the opening of the mackerel trawls, the occurrence of mackerel in the stomachs of two pilot whales taken in the Atlantic mackerel fishery, and the high incidence of mortality in the Atlantic mackerel fishery. It is possible, however, that feeding on Atlantic mackerel is an opportunistic phenomenon related to fisheries only, and that pilot whales do not otherwise prey significantly on mackerel.

Sex and maturity of common dolphins and pilot whales taken in foreign fishing operations

It is likely that most of the common dolphins killed in the *Loligo* and Atlantic mackerel fisheries were sexually immature. Estimates of total length at sexual maturity for male common dolphins are extremely variable between populations (Hui 1979, Perrin and Reilly 1984, Collett and Saint-Girons 1984). Collett and Saint-Girons (1984) found that, in the northeast Atlantic, sexual maturity in male common dolphins is reached at 200 cm, with animals <190 cm prepubescent. Several species of dolphins, including common dolphins, are known to travel in herds segregated by age and sex. In the northwest Atlantic, segregation by age and sex has been found in bottlenose dolphins (Irvine et al. 1981, Shane et al. 1986) and the harbor porpoise (Gaskin 1982). Irvine et al. (1981) found that subadult males formed bachelor groups, and sexually mature adult males rarely mixed with subadult males. Also, male and subadult female dolphins may follow fishing nets more often than females with calves. The dolphins reported in Table 6 were not captured simultaneously (i.e., having come from one group or pod) but rather were captured on several separate occasions. Although female common dolphins with calves have been observed in the areas of foreign fishing activity, none have been captured during trawling operations.

The size/sex composition of pilot whales killed in the Atlantic mackerel fishery indicates that most of the animals were sexually mature females. The size and sex ratios of pilot whales killed in the Atlantic mackerel fishery are similar to those ratios observed from pilot whale mass strandings in New England waters (Greg Early, New England Aquarium, Boston, MA, pers. commun., May 1988). Pilot whales are gregarious and social groupings are believed to be comprised of several sexually mature females and a few mature males (Martin et al. 1987).

Incidental take of common dolphins and pilot whales relative to available abundance estimates for each species

Estimates of the total number of common dolphins and pilot whales are available both for the shelf-edge alone and the combined all-shelf and shelf-edge waters of the northeastern United States (an area which is contained within the EEZ) by season (CETAP 1982). These estimates are based on standardized aerial surveys conducted during November 1978–January 1982, using line-transect methodology. Although these estimates are not for the same time period as the majority of the incidental take described in this paper, and these estimates have very high degrees of uncertainty (e.g., standard deviations of the estimates equal to the estimates themselves), they are the only population estimates available which can provide an indication of the relative magnitude of these incidental takes.

The shelf-edge abundance estimate for common dolphins during winter (most incidental takes for this species occurred during December and February) is 15,703 (CV 0.78) (CETAP 1982, table 17, p. 261). The average take per year for 1977–88 was 17 and 39 in 1984–88. These takes represent 0.11% and 0.25% of the winter abundance estimate. The maximum annual rate of take based on this winter abundance estimate was 0.48 ($n = 76$) in 1986 and was nearly twice the 1984–88 average.

Similar CETAP shelf-edge estimates for pilot whales during spring and summer are 6823 (CV 0.52) (spring) and 5251 (CV 079) (summer) (CETAP 1982, table 15, p. 233). The average take per year for 1977–88 was 25 and 46 in 1984–88. These takes represent 0.37% and 0.67% (spring) and 0.48% and 0.88% (summer) of the average seasonal abundance estimates for this species. The maximum annual rate of take based on the spring and summer abundance estimates, respectively, were 2.01% and 2.70% ($n = 142$) in 1988 and were three times the 1984–88 spring and summer rates of take.

The shelf-wide abundance estimates for common dolphins 31,124 (CV 0.59) (winter), and pilot whales 11,417 (CV 0.37) (spring) and 9808 (CV 0.66) (summer) are nearly twice the shelf-edge estimates, which reduces the above estimated rates of incidental take by nearly 50% if animals from the shelf-edge and shelf are considered as a single population.

To place pilot whale takes within the EEZ in perspective, present pilot whale incidental kill levels are comparable with recent mass strandings in New England waters (Greg Early, New England Aquarium, Boston, MA, pers. commun., May 1988). They do not approach the mortalities reported by Mercer (1975) for the historical Newfoundland drive fisheries (1948–71: Total 54,248; average 2260/yr). The impact of trophic

changes in the offshore cetacean communities, and the unknown DWF incidental mortality levels on components of the dolphin stocks when the DWF is fishing outside the EEZ, may be more of a factor in structuring present dolphin population trends than the levels of incidental takes that occur within the EEZ.

Also, we do not know the historical rates of take during the period 1960–76, when over 100 fishing vessels operated inside the EEZ per year. Since these fleets were not restricted by time or space, it is not unreasonable to assume that the number of dolphins taken pre-MFCMA were equal to or greater than the present. However, extrapolation of current levels of take to historical DWF fishing effort off the U.S. east coast (beyond speculation) would not be appropriate for several reasons. These include differences in the spatial/seasonal components of the fisheries over time and changes in the principal targeted species that have occurred during the past several decades. Likewise, the marine mammal/finfish/squid associations might have, likewise, changed during this time period. Also, technological changes in fishing gear and vessels have improved greatly during the past two decades, which might have increased the rate of take in recent years. Changes in the nationalities, and their associated fishing techniques, represented in the DWF have also occurred and could effect the rate of take of mammal species.

Acknowledgments

We thank Doug Beach, Steve Murawski, Tom Polacheck, Tim Smith, and two anonymous referees for reviewing this manuscript. We acknowledge and thank the foreign fishery observers for collecting the incidental take data, and their dedication to obtaining biological samples.

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Abstract.—A study was made of age, growth, and reproduction of the king mackerel *Scomberomorus cavalla* in Trinidad waters captured by hook-and-line and drift gillnets. Ages, estimated from otolith rings, ranged from 0 to VII in males and from 0 to X in females. Mean back-calculated lengths in 99 males ranged from 43.7 cm FL at the end of year I to 85.9 cm FL at the end of year VI, and in 233 females from 41.8 cm FL at the end of year I to 105.6 cm FL at the end of year VIII. The von Bertalanffy growth equations were for males, $L_\infty = 112.3\,[1 - \exp(-0.18(t + 1.80))]$ and for females $L_\infty = 140.1\,[1 - \exp(-0.15(t + 1.52))]$. Based on gonad examination of 97 males and 224 females, spawning takes place throughout the year around the island, with peak spawning from October through March, a period associated with low salinity. First spawning takes place at ages I–II for both sexes. Females predominated in all size groups, with the proportion of males increasing during the peak spawning season.

Manuscript accepted 11 December 1989.
Fishery Bulletin, U.S. 88:361–370.

Age, Growth, and Reproduction of the King Mackerel *Scomberomorus cavalla* (Cuvier) in Trinidad waters

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The king mackerel *Scomberomorus cavalla* (Cuvier) (Scombridae) occurs in coastal waters of the western Atlantic ranging from the Gulf of Maine to Rio de Janiero (Briggs 1958). It has also been reported throughout most of the West Indies (Erdman 1949), and its distribution is said to extend eastwards to Africa (Jordan et al. 1930). However, more recent reviews (Collette and Russo 1979) make no mention of *S. cavalla* in the Eastern Atlantic, although it has been reported from St. Paul's Rocks, a group of small islands in the mid-Atlantic (Lubbock and Edwards 1981).

Scomberomorus cavalla has commercial and recreational value throughout its range. Griffiths (1971) considered *Scomberomorus* spp., especially *S. cavalla* and *S. maculatus* (= *S. brasiliensis* Collette et al. 1978) to have greater commercial potential than the tunas in Venezuela. The general biology of *S. cavalla* has been investigated in North American waters (Beaumariage 1973) and off the state of Ceara, northeastern Brazil, including age and growth studies (Nomura and Rodrigues 1967, Ximenes et al. 1978). Manooch et al. (1978) provided a useful annotated bibliography on this species, and many aspects of its biology and fishery have been summarized by Collette and Russo (1984). More recent work includes studies on reproduction (Finucane et al. 1986) and growth (Manooch et al. 1987) in North American waters.

In Trinidad, Whiteleather and Brown (1945) and more recently Sturm et al. (1984) reported that *S. cavalla* approached *S. maculatus* (= *S. brasiliensis*) as the most abundant continental pelagic species in commercial landings. The *Scomberomorus* fishery in Trinidad is artisanal and seasonal from March through October, and *S. cavalla* is caught mainly by hook-and-line (trolling and live-bait fishing) and drift gillnets (Sturm et al. 1984). This paper provides information on age, growth, and reproduction of *S. cavalla* (the kingfish or thazard) in Trinidad waters.

Materials and methods

The climate of Trinidad is tropical, with a wet season from June to December. The surrounding waters are mainly estuarine. Surface temperatures vary little, ranging from 27 to 29°C (van Andel and Postma 1954, Edwards 1983). Further details of the study area may be found in Sturm (1978).

Fish were bought from artisanal fishermen in 1981–82 at six beaches: Maracas and Las Cuevas in the north, Mayaro and Guayaguayare in the southeast, and Cedros and Icacos in the southwest of the island. Artisanal catches consisted mainly of both *Scomberomorus* species, which on being landed were separated into baskets. There were usually not more than about a dozen boats fishing on any

one day from a beach, and catch per boat of *S. cavalla* was usually small (<20 fish). Not more than three catches were sampled up to a maximum of about 25 fish per sampling day, to enable accuracy of sample treatment in the field. Entire catches were sampled, and when this was not possible, large fish (>90 cm FL) and/or small fish (<50 cm FL), when present, were selected to direct attention to the ends of the distribution, and the rest of the sample was taken at random. A total of 363 fish was obtained, 190 from hook-and-line, 165 from gillnets (average stretched mesh size 113 mm), and eight from beach seines. In addition, 264 fish were measured at the Port of Spain Fish Market. Fish were measured to the nearest 0.5 cm fork length (FL) and weighed to the nearest 20 g. Gonads were weighed to the nearest 10 g.

Otoliths (sagittae) were used to age *S. cavalla*. When viewed in a black dish containing water in reflected light under a binocular microscope (×10), the otoliths revealed opaque and translucent rings. The non-marginal opaque rings were counted as annuli following Beaumariage (1973), Ximenes et al. (1978), Johnson et al. (1983), and Manooch et al. (1987), and distances were measured along the longitudinal axis from the focus to the distal edge of each opaque ring and to the edge of the otolith. One person read the otoliths.

The relationship between fork length and otolith radius was determined by regression analysis using both linear and quadratic models. When the relationship was established, fork length at age was back-calculated using methods of Bagenal and Tesch (1978).

The von Bertalanffy growth equation (1938)—$L_t = L_\infty [1 - \exp(-K(t + t_0))]$ where L_t = fork length at age t, L_∞ = asymptotic fork length, K = growth coefficient, and t_0 = time when length is theoretically zero—was fitted to weighted mean back-calculated lengths using an MS-DOS/BASIC version of a computer program by Sparre (1987).

Macroscopic stages of gonad development for both sexes were identified as described for *S. maculatus* (= *S. brasiliensis*) by Sturm (1978). They were immature-inactive, immature-developing, ripe, and ripe-running. The gonadosomatic index (GSI) was computed by dividing gonad weight by total fish weight and multiplying by 100.

Results

Size composition of material examined

Length frequencies of *Scomberomorus cavalla* samples from gillnets and hook-and-line were approximately similar. Hook-and-line apparently selected slightly larger fish—45–114.5 cm FL, with a modal length between 66 and 70 cm FL—than gillnets, which selected fish between 38.5 and 105 cm FL, with a modal length of between 61 and 65 cm FL (Fig. 1). The largest fish sampled was a 127-cm FL female caught in a beach seine. The size range of fish measured at the Port of Spain Fish Market was 37–135 cm FL with a modal length of 61–65 cm FL.

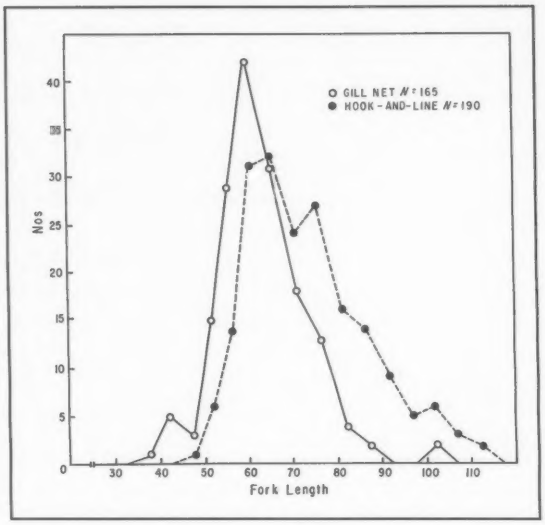

Figure 1
Length frequencies of gill net and hook-and-line samples of *Scomberomorus cavalla* from Trinidad waters. Lengths are grouped into 5-cm intervals. N = number of fish sampled.

Age and growth

Only 2 of 341 otoliths were considered illegible. However, not all of the remaining 339 otoliths had clear rings, though 85% were read with confidence. The main difficulty was determining the extent of the first opaque ring. The remaining 15% (52) were reread, with 79% (41) agreement between the two readings. The remaining 11 otoliths were then given new readings. For tracing the frequency of opaque-edged otoliths throughout the year, the data were grouped in bimonthly intervals due to the scarcity of data in non-seasonal months (Fig. 2). Otoliths with opaque edges were found throughout the year. The minimum percentage (20%) occurred in August–September after which there was a large increase to maximum percentages (60%, 58%, and 57%) from October through March, followed by 36% and 35% in April–May and June–July, respectively. These results suggest that opaque rings are formed

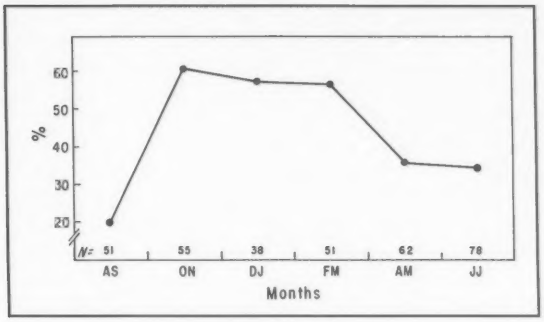

Figure 2
Bimonthly percentages of otoliths of *Scomberomorus cavalla* with opaque edges. N = number of fish sampled.

annually, mainly from October through March. Time of ring formation is similar to that recorded for Brazilian *S. cavalla* (Ximenes et al. 1978).

The relationship between fork length (FL) and otolith radius (OR) was represented by the following linear equations:

$$\text{Males: } FL = -1.73 + 1.49OR \ (r = 0.86)$$
$$\text{Females: } FL = -11.64 + 1.76OR \ (r = 0.90)$$

The intercepts were significantly different at the $P<0.001$ level ($F = 14.76$, df = 1, 336); therefore, the data were treated separately. Second-degree quadratic models were fitted to the separate data, but analysis of variance did not show significant curvature for males ($F = 3.03$, df = 1, 98, $P>0.05$) nor females ($F = 1.65$, df = 1, 235, $P>0.1$), therefore the linear equations were used to back-calculate length from age for males and females separately.

Observed and back-calculated lengths for 99 male and 233 female *S. cavalla* are shown in Table 1. Five age-0 fish (38.5–57.5 cm FL) were also recorded. The oldest male was age VII and the oldest female age X, but these were not included in the back-calculations. Length variation within age groups was large, as was the case for southeastern United States populations (Beaumariage 1973, Johnson et al. 1983). For example, age-II females ranged from 43.0 to 85.5 cm FL. From age II onwards, females grow faster than males. Figure 3 compares back-calculated growth of *S. cavalla* from Trinidad with that from southeastern United

Table 1
Mean observed and back-calculated lengths (cm) for *Scomberomorus cavalla* from Trinidad waters.

Age group	N	Mean observed length	Range	Mean back-calculated length at age							
				I	II	III	IV	V	VI	VII	VIII
Males											
I	23	57.3	44.0–72.5	44.9							
II	34	64.5	53.5–75.0	42.5	57.8						
III	25	71.4	62.5–78.0	44.6	58.4	66.9					
IV	9	72.2	65.5–81.0	41.5	54.5	61.8	68.3				
V	6	81.8	77.5–86.5	44.2	58.1	67.5	73.6	78.8			
VI	2	87.5	80.5–94.5	46.4	58.5	68.9	74.6	81.0	85.9		
Weighted mean				43.7	57.6	66.0	70.9	79.3	85.9		
N				99	76	42	17	8	2		
SD				5.0	5.3	5.2	5.5	4.3	9.8		
Annual increment					13.9	8.4	4.9	8.4	6.6		
Females											
I	46	58.2	42.0–70.5	43.7							
II	68	67.4	43.0–83.5	42.3	59.7						
III	48	71.8	62.0–93.5	39.8	57.1	66.7					
IV	33	80.2	65.0–101.0	41.1	57.6	67.4	75.1				
V	19	87.2	77.5–103.0	42.2	58.0	68.7	76.7	83.8			
VI	7	95.8	92.0–101.5	43.2	60.1	70.5	78.6	85.7	91.5		
VII	7	102.9	92.5–109.0	41.6	62.2	73.4	81.5	87.5	92.7	99.2	
VIII	5	109.7	101.0–127.0	39.9	59.8	70.0	79.6	88.4	95.8	101.2	105.6
Weighted mean				41.8	58.6	68.0	76.8	85.1	93.1	100.1	105.6
N				233	187	119	71	38	19	12	5
SD				5.7	6.2	7.0	6.8	6.2	5.4	1.9	9.9
Annual increment					16.8	9.4	8.8	8.3	8.7	7.0	5.5

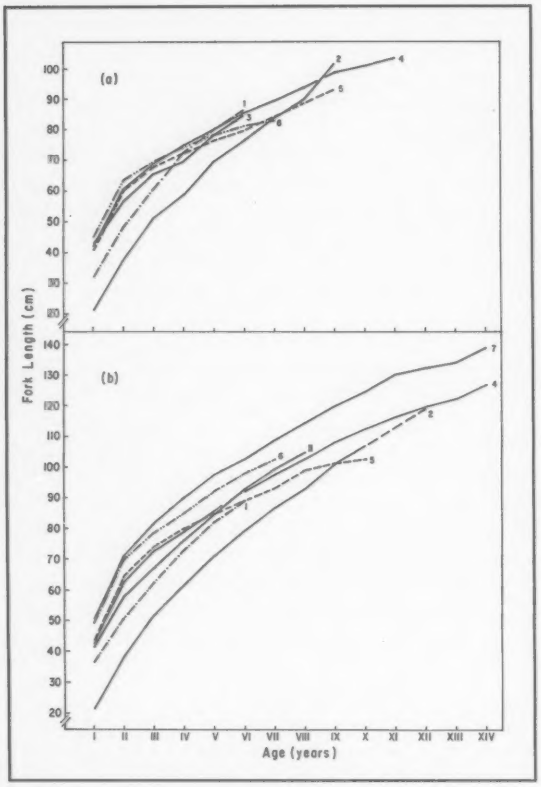

Figure 3

Growth (mean back-calculated fork lengths) of *Scomberomorus cavalla* (a) males and (b) females. 1 = Northeastern Brazil (Ximenes et al. 1978); 2 = Northeastern Brazil (Nomura and Rodrigues 1967), ages III and above observed lengths; 3 = Trinidad, this study; 4 = U.S. Gulf of Mexico (Manooch et al. 1987); 5 = Southeastern U.S., excl. La. (Johnson et al. 1983); 6 = Florida (Beaumariage 1973), fork length transformed from standard length by his formula FL = 1.096SL – 17.143; 7 = Southeastern U.S. incl. La. (Johnson et al. 1983).

States and northeastern Brazil. For both sexes, there is wide separation of lengths at age I, with those of Trinidad and North American fish being larger than those of Brazilian fish. The largest male lengths are from the Florida sample (Beaumariage 1973) up to age IV, and the smallest are for fish sampled in Brazil by Nomura and Rodrigues (1967) up to age VI. For females, the largest lengths are again for Beaumariage's sample except for an anomalous population of large females sampled in Louisiana (Johnson et al. 1983), and the smallest lengths are similarly for Nomura and Rodrigues' Brazilian sample. Back-calculated lengths at age of Trinidad fish lie between the larger lengths of North American fish and the smaller lengths of Brazilian fish, up to age III for males (82.8% of the sample) and age V for females (91.9% of the sample). The growth curve of Trinidad males closely resembles those from the southeastern United States presented by Johnson et al. (1983) and Manooch et al. (1987) up to age V, whereas the growth of Trinidad females is more similar to that of Brazilian females sampled by Ximenes et al. (1978). Growth rates of males from the different areas are similar up to age II, with Brazilian males showing less incremental decrease in the later ages. The same trend is shown for females, with marked incremental decrease being shown by southeastern United States (excluding Louisiana) females sampled by Johnson et al. (1983).

The von Bertalanffy growth parameters of Trinidad *S. cavalla* are presented in Table 2 along with those from southeastern United States and Brazil. Asymptotic lengths are larger for females than males. The asymptotic lengths of Trinidad and Brazil males are close, and much larger than those from North America, except for the recent study from the Gulf of Mexico (Manooch et al. 1987). For females, the pattern is somewhat similar, with the Trinidad and Gulf of Mexico values being the largest, except for the additional sample of large females from Louisiana (Johnson et al. 1983). For both sexes the K values are fairly close, the lowest coming from Trinidad, Brazil, and the Gulf of Mexico, with again the exception of the Louisiana females.

Size and age at first maturity

There were 14 ripe males (11 ripe + three ripe-running) and three ripe females in the age-I group, indicating first spawning for both sexes to take place in this age group. The shortest ripe male was 54.5 cm, and the largest immature developing male was 80 cm. The shortest ripe female was 58.5 cm, and the largest immature developing female was 114.5 cm. These sizes at maturity indicate that first spawning for both sexes may also take place at age II (Table 1).

Gonad analysis and GSI

Gonad stages and corresponding GSI values are shown in Table 3. No ripe-running females nor spent fish were observed in this study. Figures 4 and 5 show gonad analysis of the 97 males and 224 females that were capable of spawning as indicated by size at first maturity. Of these, 70 males and 164 females were analyzed for GSI, and the results are also shown in Figures 4 and 5. Male gonad analysis was more difficult because milt was present in the early stages of gonad development; this explained the trend to higher percentages of ripe males. Ripe fish were present during all months

Table 2
von Bertalanffy growth parameters for *Scomberomorus cavalla* from Trinidad, southeastern United States, and Brazil.

Area and source	L_∞ (FL cm)	K	t_0 (yr)
Males			
Trinidad (this study)	112.3	0.180	−1.79
Northeastern Brazil (Nomura and Rodrigues 1967)	116.0	0.180	−0.22
Northeastern Brazil (Ximenes et al. 1978)	113.3	0.229	−1.50*
Florida (Beaumariage 1973)	90.3**	0.350	−2.50
Southeastern U.S. (Johnson et al. 1983)	96.5	0.280	−1.17
U.S. Gulf of Mexico (Manooch et al. 1987)	111.3	0.208	−1.48
Females			
Trinidad (this study)	140.1	0.150	−1.52
Northeastern Brazil (Nomura and Rodrigues 1967)	137.0	0.150	−0.13
Northeastern Brazil (Ximenes et al. 1978)	131.7	0.164	−2.00*
Florida (Beaumariage 1973)	124.3**	0.210	−2.40
Southestern U.S., excl. La. (Johnson et al. 1983)	106.7	0.290	−0.97
Southeastern U.S., La. (Johnson et al. 1983)	152.9	0.140	−2.08
U.S. Gulf of Mexico (Manooch et al. 1987)	141.7	0.136	−1.98

*Assumed negative.
**Calculated from Beaumariage's formula FL = 1.096SL − 17.143.

Table 3
Gonad stages and gonadosomatic indices of *Scomberomorus cavalla* from Trinidad waters.

	Males			Females		
Gonad stage	*N*	Mean GSI	Range GSI	*N*	Mean GSI	Range GSI
Immature inactive	2	0.77	0.32–1.37	10	0.58	0.41–1.16
Immature developing	21	0.38	0.14–0.78	113	0.63	0.16–1.37
Ripe	18	0.92	0.30–1.92	41	1.75	0.41–5.68
Ripe running	29	1.11	0.33–3.73	—	—	—

except December (when only nine fish were sampled), and ripe females were absent in April. Maximum percentages of females occurred from September to October and January to March. GSIs for females peaked in September, November, January, and February. Males showed similar patterns, though data were more limited. The above observations indicated that *S. cavalla* spawns throughout the year with more intense spawning from September through March.

Sex ratio

Females were dominant in all size groups, both in gillnet and hook-and-line samples, and in the peak spawning and non-peak spawning seasons (Table 4). The degree of dominance varied with size class, type of gear, and season. Dominance increased with size class, and all but a single specimen over 90 cm FL was female. Females predominated to a greater extent in the hook-and-line samples compared with gillnet samples. In gillnet samples, the proportion of females decreased from 74% during the non-peak spawning season to 62% during the peak spawning season, which corresponded with an overall decrease in females from 77% to 63% in the respective seasons. In the southeastern United States, the sex ratio was also found to favor females (Fischer 1980, Trent et al. 1983).

Discussion

Evidence for time of annulus formation in Trinidad *Scomberomorus cavalla* is weak. Tracing of otolith edges throughout the year suffered from a paucity of

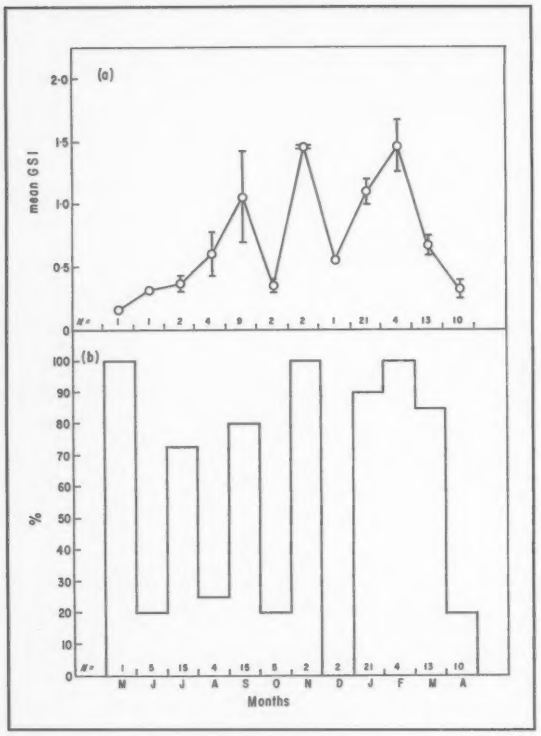

Figure 4

Seasonal maturation cycle of male *Scomberomorus cavalla* (>54.5 cm) by (a) mean monthly GSI and (b) monthly percentages of ripe (ripe and ripe-running) gonads. N = number of fish sampled.

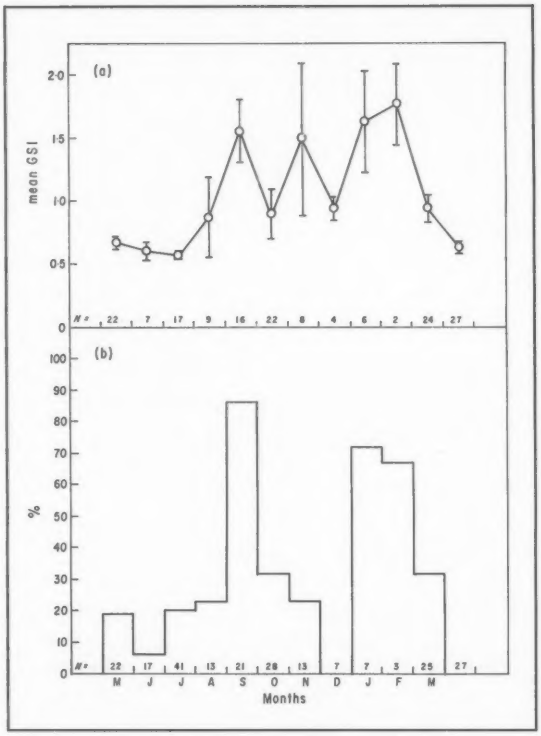

Figure 5

Seasonal maturation cycle of female *Scomberomorus cavalla* (>58.5 cm) by (a) mean monthly GSI and (b) monthly percentages of ripe gonads. N = number of fish sampled.

data when the annulus is apparently formed as fish were scarce from November to February. Maximum (bimonthly) percentages of opaque otolith margins compare well with those (monthly) of North American studies (Beaumariage 1973, Johnson et al. 1983, Manooch et al. 1987). However, in the present study the minimum (bimonthly) percentage (20%) was much higher than in North America where in all the studies there were one or more months with no edged otoliths. In Trinidad the period September to March, when maximum percentages of opaque otolith margins are found, corresponds with the period of greatest spawning intensity. In Brazil, the opaque ring is laid down from November to March corresponding to a period of intense spawning (Ximenes et al. 1978). Otoliths of North American fish generally had the largest percentages of opaque margins from April through June (Beaumariage 1973, Johnson et al. 1983, Manooch et al. 1987) at the start of a well-defined spawning season (Beaumariage 1973, Finucane et al. 1986). The process of spawning may therefore be related to annulus formation in *S. cavalla*. If first spawning takes place at age II, as might occur on occasion for Trinidad *S. cavalla*, an annulus in immature (age-I) fish may be explained by some internal physiological rhythm, together with the environmental changes that trigger spawning, causing annulus formation. This explanation was put forward for annulus formation in immature fish for hake *Merluccius merluccius* (Hickling 1935) and red snapper *Lutjanus campechanus* (Nelson and Manooch 1982). As spawning is year-round in the tropical waters around Trinidad, the finding of relatively large numbers of opaque margined otoliths in the months outside the period of their maximum occurrence during peak spawning can be expected. These, however, obscure the results of tracing the frequency of otolith edges throughout the year compared with the more clear-cut results from the more temperate North American waters.

The differences in length at age and theoretical growth parameters between Trinidad, Brazilian, and North American fish may result from different environ-

Table 4
Sex ratio of *Scomberomorus cavalla* from Trinidad waters.

Length range (cm)	Gillnets			Hook-and-line			Totals		
	Male	Female		Male	Female		Male	Female	
	(*N*)	(*N*)	(%)	(*N*)	(*N*)	(%)	(*N*)	(*N*)	(%)
Peak spawning (September–March)									
30.0–49.5	1	0	0	0	1	100			
50.0–69.5	24	36	60	10	24	71			
70.0–89.5	18	12	40	9	29	76			
90.0–109.5	0	1	—	1	11	92			
110.0–130.5	0	0	—	0	0	—			
Total	43	49	53	20	65	76	63	114	60
Non-peak spawning (April–August)									
30.0–49.5	1	6	86	0	0	—			
50.0–69.5	14	39	74	14	26	65			
70.0–89.5	4	7	64	8	42	84			
90.0–109.5	0	2	100	0	13	100			
110.0–130.5	0	0	—	0	2	100			
Total	19	54	74	22	83	79	41	137	77
Totals	62	103	62	42	148	78			

ments, feeding habits, exploitation rates, methods of capture, sample sizes, etc. The fishery in North America is better developed than in Brazil (Collette and Russo 1984) and Trinidad, which enabled larger samples for age and growth studies to be collected from the former region. There were considerable differences between sample sizes of older fish in the various studies, which could introduce bias in the comparison of von Bertalanffy parameters. Best representation of growth of older fish came from Manooch et al. (1987) and the anomalous group of Louisiana females (Johnson et al. 1983). Changes in populations between studies brought about by exploitation and other factors could also influence the results.

Different methodologies could also contribute to these differences. Nomura and Rodrigues (1967) counted translucent rings to age Brazilian fish, thus omitting part of a year. This probably resulted in their obtaining the slowest growth of all the studies. Back-calculated lengths were fitted to the von Bertalanffy equation by Ximenes et al. (1978), Johnson et al. (1983), and in this report. Beaumariage (1973) fitted observed standard lengths and advised caution in extrapolation of the theoretical growth curve for size at older ages, because it was derived from Walford plots that excluded older fish; this resulted in conservative estimates. Nomura and Rodrigues (1967) used both back-calculated and observed lengths, which probably resulted in large values of L_∞. Other differences in methodology, e.g., the weighting of mean back-calculated and observed lengths and more exact fitting of the von Bertalanffy curve using computer programs in the later studies, and the non-use of an intercept value for back-calculation in some of the studies, could lead to minor differences in the results. Comparisons of results between the three areas evidently cannot be properly done due to differing sample sizes and methodologies.

Estimates of maturity of 58.5 cm FL or age I–II for Trinidad female *S. cavalla* generally agree well with those of other studies. In Brazil, first maturity was found to take place at 58.6 cm FL (Alves and Tome 1967) and 63.5 cm FL or age III (Gesteria and Mesquita 1976). Another study showed that females first matured between 43.5 and 56.5 cm FL or age III, with 50% maturity at 77 cm FL or age V–VI (Ivo 1972). Size of maturity of Trinidad females compares well with that in Brazil. However, greater age at maturity of Brazilian fish could be due to overestimated age at length based on the use of translucent rings for ageing by Nomura and Rodrigues (1967). Finucane et al. (1986) reported size at maturity at 44.9 cm FL in the southeastern United States. In Florida waters, Beaumariage (1973) round ripe eggs in age-I females (61.4 cm SL = 65.6 cm FL) similar to Trinidad results. However, he concluded that these eggs were aborted or reabsorbed, and spawning did not really take place until age IV (88.0 cm FL). As with females, ripe males

first appeared at age I (63.4 cm FL) as they did in Trinidad, but Beaumariage believed that males spawned initially at age III (77.0 cm FL) due to the greater development of spermatogenesis in the testes of older fish. However, in Trinidad initial spawning takes place at age I, as shown by the presence of ripe-running males in this age group.

The spawning pattern of *S. cavalla* in Trinidad is apparently similar to that off the coast of Ceara, in northeastern Brazil. Gesteria and Mesquita (1976) observed year-round spawning with maximum intensity from October through March, as in Trinidad. Spawning throughout the year was also recorded by Ivo (1972), but his period of maximum activity was from January through June. Another study (Menezes 1969) indicated that they spawn during the period October through March. Further north, the spawning season is reversed, where in the northeastern Caribbean it lasts from April through November (Erdman 1976) and in the southeastern United States, from April through October (Beaumariage 1973, Finucane et al. 1986). Spawning migrations in North America are determined by temperature (Moe 1972, Beaumariage 1973). In Trinidad, however, spawning and migration may be influenced by salinity changes because there is little variation in the water temperature. Peak spawning starts after the rains have set in, and may be triggered by a drop in salinity; minimum salinities have been recorded in August and September (van Andel and Postma 1954, Edwards 1983). The presence of ripe-running males in the samples indicates spawning in local waters, but the spawning grounds remain to be discovered. The scarcity of the fish during November through February remains unexplained. Spawning on the outer Continental Shelf, 50–60 km offshore, as occurs in the northwestern Gulf of Mexico (McEachran et al. 1980) would place part of the population beyond the reach of the artisanal fishing fleet which is limited to some 40 km offshore. Another possible factor could be migration along the Venezuelan coast to the northwest and/or the southeast, although part of the population may be resident throughout the year. Decreased vulnerability to hook-and-line due to decreased feeding activity during spawning, and/or gillnets due to spawning in waters deeper than that in which the gillnet is effective, are other possible reasons to be considered.

Beach landing data indicate that a southerly migration takes place in Trinidad during the months when the fish is seasonally abundant (Sturm et al. 1984). In the present study, gonad analysis did not suggest any migratory trends since ripe fish were taken around the coast throughout the year. Moreover, observations on stomach contents showed no clear feeding patterns as evidence of migration (unpubl. data). The spawning and abundance patterns of *S. cavalla* approximately correspond to those of *S. maculatus* (= *S. brasiliensis*), which spawns throughout the year with more intense spawning from October through April and is seasonally abundant from May through September (Sturm 1978). *S. brasiliensis* also moves in a southerly direction during peak abundance, part of likely clockwise movements around the island (Sturm 1978, Sturm et al. 1984). In Florida, Williams and Sutherland (1979) and Sutherland and Fable (1980) have shown that *S. cavalla* undertakes long-range migrations compared with the shorter range migrations of *S. maculatus*, which is closely related to *S. brasiliensis* (Collette et al. 1978). In Trinidad, a similar situation would explain the difficulty in recognizing migratory trends of *S. cavalla*, compared with the more local movements described for *S. brasiliensis* (Sturm 1978).

Female dominance in samples may be the result of more females than males being hatched or mortality being higher in males than females. Higher mortality probably is associated with slower growth in males. Alternatively, female dominance may be a function of gear selection in gillnets or of behavioral differences between the sexes. Increased voracity in females was recorded in Brazil (Menezes 1969) and may explain why the sex ratio favored females in hook-and-line samples. Also, males may inhabit greater depths than females and are less vulnerable to gillnets. If this was the case, a meeting of the sexes for spawning by an upward migration of males and/or a downward migration of females could explain the increase in the male:female ratio observed for gillnets during peak spawning.

Acknowledgments

Thanks are due to Michèle Julien-Flüs for assistance in field work, to Sherry Manickchand-Heileman for useful comments and discussion, to Bruce Lauckner of the Caribbean Agricultural Research and Development Institute for advice on statistical matters, to Rodney Ramkissoon for assistance in figure preparation, and to Avril Siung-Chang and Roland Bailey (Kings College, London University) for reading the manuscript.

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Abstract.—Leopard shark tag recovery data, obtained from a 1979–88 study in San Francisco Bay, were analyzed to determine temporal and geographic distribution of the tagged population. Virtual population analysis of the tag recovery data was used to derive fishing mortality rates, which in turn were used to obtain yield-per-recruit and stock replacement values, and to estimate the effect of management by size limit on stock replenishment and yield per recruit.

Of the tagged population, 11% was recovered by sport anglers and commercial fishermen, and the distribution of recoveries indicates that leopard sharks are mostly resident in San Francisco Bay, although a portion of the population moves out of the Bay during fall and winter. An unusually high number of recaptures was made in 1983, a year of El Niño conditions and high river run-off. After obtaining mortality, yield, and stock replacement values, it was proposed that a viable management strategy for the San Francisco Bay leopard shark would be a size limit of 100 cm or 40 inches to ensure maintenance of the stock and provide a yield per recruit not too far below a maximum.

Manuscript accepted 19 January 1990.
Fishery Bulletin, U.S. 88:371–381.

Leopard Shark *Triakis semifasciata* Distribution, Mortality Rate, Yield, and Stock Replenishment Estimates Based on a Tagging Study in San Francisco Bay

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Shark has now become a familiar item at seafood counters and on restaurant menus in the United States (Slosser 1987), while in the past these fish were often discarded as trash fish, or at best valued for fish meal or their vitamin A-rich livers (Frey 1971). California has seen the rise of four new commercial elasmobranch fisheries since the mid-1970s (Holts 1988), and recreational shark fishing has grown in popularity in California and in other coastal states (Ristori 1987). The relatively rapid increase in shark harvesting has created a pressing need for more biological information to support management of targeted species, particularly information relating to population structure, mortality and replenishment rates, and degree of exchange between stocks. Elasmobranchs may be particularly vulnerable to exploitation, because they are generally slow growing and produce relatively few young, with recruitment appearing to be largely determined by parental stock size (Holden 1977).

The leopard shark *Triakis semifasciata* is harvested both commercially and recreationally in California. It occurs along the coast from Baja California, Mexico, to Oregon, and is very common in northern California bays (Squire and Smith 1977, Eschmeyer et al. 1983). Its fairly large size (maximum recorded is 180 cm; Kato et al. 1967) and accessibility in nearshore areas and bays probably contribute to its appeal with anglers and small-scale commercial boat operators. Reported commercial landings in California since 1980 have ranged from 18,199 kg (40,085 lbs) in 1980 to 45,994 kg (101,309 lbs) landed in 1983 (Table 1), with the San Francisco area contributing a large portion of the catch. Recreational landings are comparatively larger, judging from estimates of landings compiled by the U.S. Department of Commerce Pacific Coast Marine Recreational Fishery Statistics Survey (Table 2). Recorded commercial landings of leopard sharks may be misleading, as leopard sharks are often lumped with other species under the general category "shark, unspecified." Because of this reporting bias, it is difficult to determine the full extent of the commercial harvest. Further, it should be noted that reliable data for stratifica-

Table 1

Reported commercial leopard shark landings (in kilos) by California port area. Source: Joyce Underhill, Calif. Dep. Fish Game, Long Beach, CA 90801, pers. commun., 17 May 1989.

Year	Eureka	San Francisco	Monterey	Santa Barbara	Los Angeles	San Diego	California total
1980	–	11 006	54	3 103	3 672	363	18 199
1981	94	12 334	55	5 505	3 482	1 913	23 384
1982	–	13 308	128	11 262	5 894	1 464	32 057
1983	–	33 764	202	7 218	2 632	2 177	45 994
1984	–	14 664	1 322	7 482	5 185	2 153	30 806
1985	24	8 054	7 620	8 135	8 725	1 871	34 430
1986	400	11 435	3 553	7 805	7 499	3 239	33 932
1987	741	6 684	3 523	6 357	6 113	1 720	25 138
1988*	1 263	2 367	2 038	5 161	3 728	4 357	18 914

*Preliminary.

Table 2

Reported commercial landings and estimates of the total marine recreational landings of leopard sharks in northern California, 1980–87. Recreational landings are Type A catches (observed landings) for north of San Luis Obispo County to the Oregon border, based on the Pacific Coast Marine Recreational Fishery Statistics Survey (provided by John F. Witzig, Natl. Oceanic Atmos. Adm., Natl. Mar. Fish. Serv., Silver Spring, MD 20910, 14 June 1989). Commercial landings are summed for northern California ports.

	Northern California landings	
Year	Commercial	Recreational
	(kilos)	
1980	11 060	68 682
1981	12 484	62 664
1982	13 436	7 578
1983	33 966	116 517
1984	15 986	33 610
1985	15 698	131 787
1986	15 388	158 778
1987	10 948	289 097

tion of catch and effort by moderately small time or area segments are unavailable for either the recreational or commercial fisheries. The smallest divisions for the recreational fishery are northern and southern California. For the commercial fishery, only the place of landing and not the place of catch is recorded, and effort data are nonexistent.

Information on reproduction, stock replacement rates, and stock interaction is scanty and mostly undocumented. Estimates of length at maturity for males have ranged from 70 to 119 cm and for females from 100 to 129 cm; size at birth is about 20 cm (Ackerman 1971, Compagno 1984, Kusher 1987). The gestation period is estimated at 10–12 months and parturition takes place in spring, according to Ackerman (1971) who worked with Elkhorn Slough fish in Monterey County, California. Certain other observations corroborate this. Moser and Sakanari* examined an aggregate of pooled embryos from fish taken in the fall in San Francisco Bay and the measurements formed a unimodal distribution with little variation in embryo sizes among litters, which is the expected pattern for an annual reproductive cycle. More than one mode among litters would be observed for a gestation period of 2 or more years. In addition, R. Russo (East Bay Park Dist., Alameda, CA 94169, pers. commun., 27 March 1984), sampling in South San Francisco Bay, has noted a predominance of pregnant females with near-term pups mainly from March through June (April–May peak), indicating a once-a-year parturition in spring. Pupping could be annual and occur in alternate years, with a 'recuperative' year between, but then about half of the mature female population would be in a nonreproductive condition at any given time. Of the 90 females over 120 cm that Ackerman (1971) examined from Elkhorn Slough, 94% had embryos or fertilized eggs in at least one ovisac; and all females >110 cm total length (TL) collected by Kusher (1987) in Elkhorn Slough and Monterey Bay and San Francisco Bay showed signs of either pregnancy, recent birth, or embryo abortion. Therefore, we use the assumption of an annual reproductive cycle in later sections dealing with stock replacement by reproduction. The leopard shark is primarily a benthic feeder (Russo 1975, Talent

*Drs. M. Moser and J. Sakanari (Long Marine Lab., Univ. Calif., Santa Cruz, pers. commun., Sept. 1984) report that in a sample of nine pregnant females taken on 10 September 1984, presumably in midterm, the mean embryo length was 11.26 cm (1.51 SD), (n = 51 embryos).

1976). Prior to the work described here, nothing was known of its movements or the degree of exchange with other leopard shark populations along the California coast.

In 1979, a tagging study was initiated in San Francisco Bay to obtain information on age validation, growth, and movements of this species. Tag recaptures were monitored over a 9-year period. This report gives results of movements that were deduced from the temporal and geographic distribution of tag recoveries. In addition, although beyond the planned design of this study, we decided to utilize the tag recovery data together with published information to estimate the effect of management by size limit on stock replenishment and on yield per recruit. The lack of suitable statistical information on catches, as mentioned previously, prevented us from performing analyses that involve weighting tag recoveries by catch or effort. Results of the age validation segment of the study have been published elsewhere (Smith 1984), and results on age and growth are also being published separately (Kusher et al. In prep.).

Methods

All sharks were tagged off Hunters Point in south San Francisco Bay in 1979. Collections were made with a 183-m longline rigged with an average of 150 baited hooks fished on the bottom at depths of 15–20 m. Prior to release, total and precaudal lengths were recorded to the nearest centimeter, and each fish was given an intraperitoneal injection of oxytetracycline hydrochloride to mark vertebral centra for age verification purposes (Smith 1984). A record was made of the sex and general physical condition of each fish; seriously injured animals were not tagged. Those with minor hook injuries or with partially everted stomachs were classified as "injured"; the rest were classified as "healthy." A plastic rototag of the type recommended by Kato and Carvallo (1967) was applied to the first dorsal fin and the fish released at the capture point. The fin tags were imprinted with a legend informing the recoverer that a reward (amount unspecified) was offered for return of the tag and the fish or a section of its vertebral column for age verification purposes. The legend also provided an address and phone number to contact to arrange delivery.

Mortality estimation

Fishing mortality rates were estimated from the tagging data using the concept described by Murphy (1965), Gulland (1965), and Tomlinson (1970), which is now commonly referred to as virtual population analysis (VPA), though it differs from the original VPA procedure of Fry (1949). The computer program COHORT, written by John Geibel and Phil Law (Calif. Dep. Fish Game, 411 Burgess Drive, Menlo Park, CA 94025) was used to calculate the estimates. The natural mortality estimate was based on Hoenig's (1983) regression equation $\log(Z) = 1.46 - 1.01 \log(t_{max})$ where Z is the instantaneous annual total mortality coefficient and t_{max} is maximum age attained by the species. If the maximum age was determined from a period when there was virtually no fishing directed at the species, then one could assume the estimated Z approximates the instantaneous annual natural mortality coefficient, M.

The basic procedure involved assuming values of M over each 1-year time interval, taking a trial value of F_n, the instantaneous annual fishing mortality coefficient, for the ultimate interval, and executing the backward VPA computation on the tag recoveries to obtain an estimate of N_0, the number of tagged fish at the beginning of the first interval. Trial values were then iterated until the series converged on N_0.

Before conducting the VPA, it was necessary to consider two additional factors which would cause adjustments to the actual observations used in the analysis: (1) the likely rate of tag loss and (2) the level of tag recovery nonreporting. Since the tagging experiment was not designed for this type of analysis, there were no built-in procedures to estimate these factors. We therefore used what we judged to be the best available information from outside sources.

Yield per recruit

Yield per recruit was calculated by piecewise integration of the yield curve. The yield in weight at each age was taken to be the product of the annual rate of exploitation, the midpoint between an individual's weights at the beginning and end of the age interval, and the population size at the beginning of the interval.

$$Y = \exp[-M(t_{r'} + 1)]\,[1 - \exp(-Z)]\,(F/Z) \times \sum_{t \geq t_{r'}}^{t_{max}} \{\exp[-Z(t - t_{r'})]\}\bar{w}_t \quad (1)$$

where Y is yield per recruit in weight (kg), t is age, $t_{r'}$ is age at first capture, and $\bar{w}_t$ is the midpoint between the weights at t and $t + 1$.

Weight at age was computed by using predicted values from the von Bertalanffy length equation from Kusher (1987) and the weight-length formula in Smith (1984). Note that equation (1) assumes constant M and Z except that natural mortality is doubled during

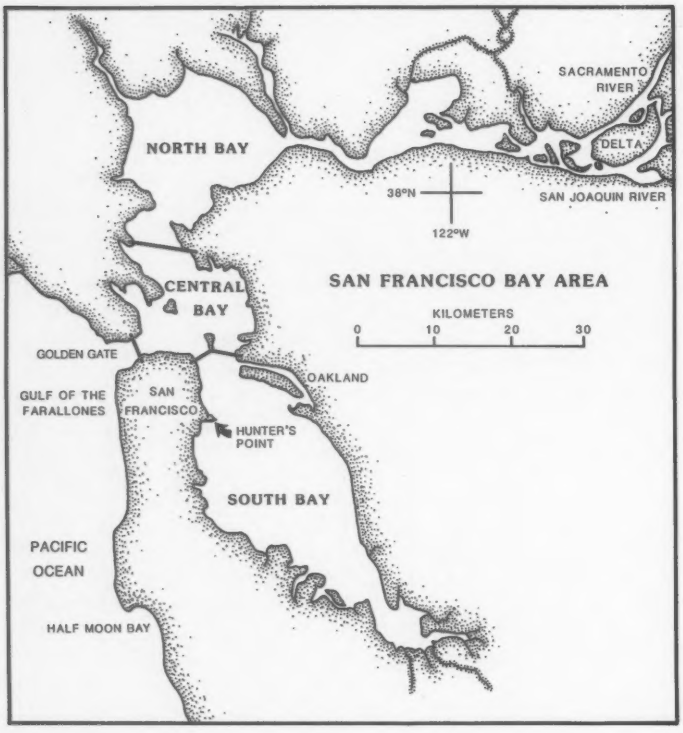

Figure 1
Map of San Francisco Bay showing location of release area (arrow) and major Bay Area divisions and names referred to in the text.

year 1. This gives some weight to a higher mortality these young fish must suffer relative to the adult sharks. The phenomenon of the young being preyed on by larger sharks has been cited by Springer (1960, 1967) and by Holden (1974).

Stock replacement

Also calculated for various levels of age at first capture (knife-edge selection) and fishing mortality were the percentages of stock which would be replaced due to reproduction. Assuming an even division among the sexes, this was done by summing over ages, from age at first maturity to maximum age, the products of the number of female survivors per recruit and the number of pups produced by females at each age above the age of maturity and multiplying this sum by 100. For given $t_{r'}$ and F

$$R = \sum_{t \geq t_m} 50 \exp[-M(t+1) - F(t - t_{r'})\, \delta]\, P_t \qquad (2)$$

where t_m is female age at maturity, R is stock replacement per recruit in percent, P_t is estimated number of progeny produced annually by an age t female, and

$$\delta = \begin{cases} 1 & t > t_{r'} \\ 0 & t \leq t_{r'} \end{cases} \qquad (3)$$

Fecundity as a function of maternal body weight was estimated by fitting a monomolecular curve of the form $P_t = \beta - \theta\rho^{w(t)}$, with P the number of progeny, $w(t)$ the weight of the female at age t, and β, θ, and ρ constants. For computation, age at maturity was taken as the age corresponding to the weight which produced a value of zero for P_t in the above equation.

Ackerman (1971, his table 6) gives the numbers of embryos observed in 66 female leopard sharks ranging in size from 9.3 to 16.3 kg. Although his data are in a form which allows only the computation of mean number of embryos per female for five weight classes, he does give the number of females observed in each weight category. Using the numbers of females as weighting factors, the curve was fitted to these means with the Levenberg-Marquardt algorithm as implemented in the NCSS nonlinear regression program*.

*Number Cruncher Statistical System, Version 5.3–Power Pack, 1988. NCSS, Kaysville, UT 84037. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Progeny as a function of maternal age was then estimated by applying the weight-length-age relationships cited above. We assume all nondeformed embryos survive to time of birth. Data were not available for applying the preferable procedure of directly regressing fecundity on age.

Geographical names and location of the tagged-fish release area are given in Figure 1.

Results

Tagging

A total of 948 sharks were tagged off Hunters Point, San Francisco, in south San Francisco Bay between 26 July and 13 September 1979. Most were tagged in August (68%) and September (26%). The hook rate was very high: 22 *Triakis* per 100 hooks, and a 44% hook rate for all elasmobranchs. Other sharks and rays taken in order of abundance were brown smoothhound *Mustelus henlei* ($n = 872$), bat ray *Myliobatis californica* ($n = 159$), soupfin shark *Galeorhinus galeus* ($n = 6$), sevengill shark *Notorhynchus cepedianus* ($n = 5$), and spiny dogfish *Squalus acanthias* ($n = 2$).

The lengths of tagged leopard sharks ranged from 51 to 144 cm TL (mean 81 cm, Fig. 2). The male:female ratio was 53:47. Large individuals may have been underrepresented in the tagging, since only 9% of females and 11% of males were over 100 cm. Commercial fishermen have reported a higher proportion of large fish in their catches, fishing at the same time with similar gear but in different areas of the south bay (B. Van Gorp and B. Fraser, commercial shark fishermen, pers. commun., June 1980). On the other hand, leopard sharks were probably recruited to our gear at a larger size than would be true for typical sportfishing tackle. Anglers fishing from shore and piers using small hooks would surely take a higher percentage of fish under 70 cm than that shown in Figure 2.

Of the 948 fish tagged, 82 individuals were classified as "injured" and the remaining 866 fish as "healthy." Return rates would presumably be higher for healthy, uninjured fish than for injured fish if the tagging operation caused mortalities; the absence of such a difference could be taken as suggestive of little or no tagging-induced mortality (Gulland 1983).

Recoveries

As of 30 September 1988, 108 fish had been recaptured of which 101 had known recapture date and location. A breakdown of all methods of recapture is given in Table 3, and provides an interesting glimpse of the various users of the leopard shark resource. The proportions reported by each group should approximate the proportions of the natural population harvested or caught by each group.

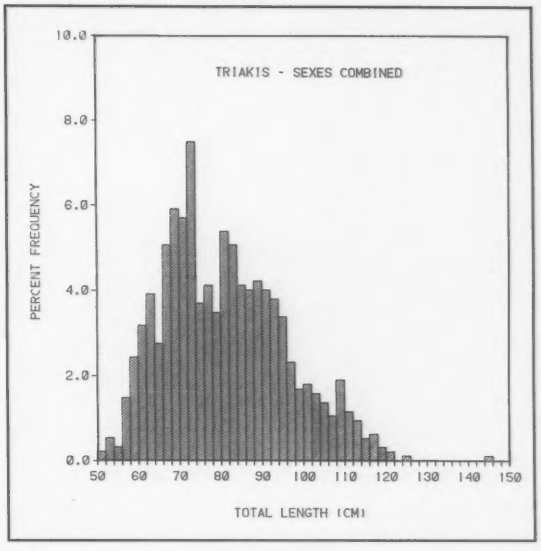

Figure 2
Length frequency of tagged leopard sharks (sexes combined) released off Hunter's Point in south San Francisco Bay, California, 1979.

Table 3
Distribution of leopard shark tag recaptures by recovery method and area in and around San Francisco Bay, California, 1979–88.

Method of recapture	Area of recapture: South bay	Central & north bays	Outside bay/ ocean	Totals
Recreational				
Private boat/skiff	32	15	1	48
Sportfishing boat (commercially operated)	0	4	0	4
Bank	13	3	2	18
Pier	10	6	0	16
Jetty	0	1	0	1
Bridge	1	0	0	1
Total	56	29	3	88
Commercial				
Bottom trawl	0	0	5	5
Gillnet	0	0	4	4
Longline	4	0	0	4
Total	4	0	9	13
Total all methods	60	29	12	101

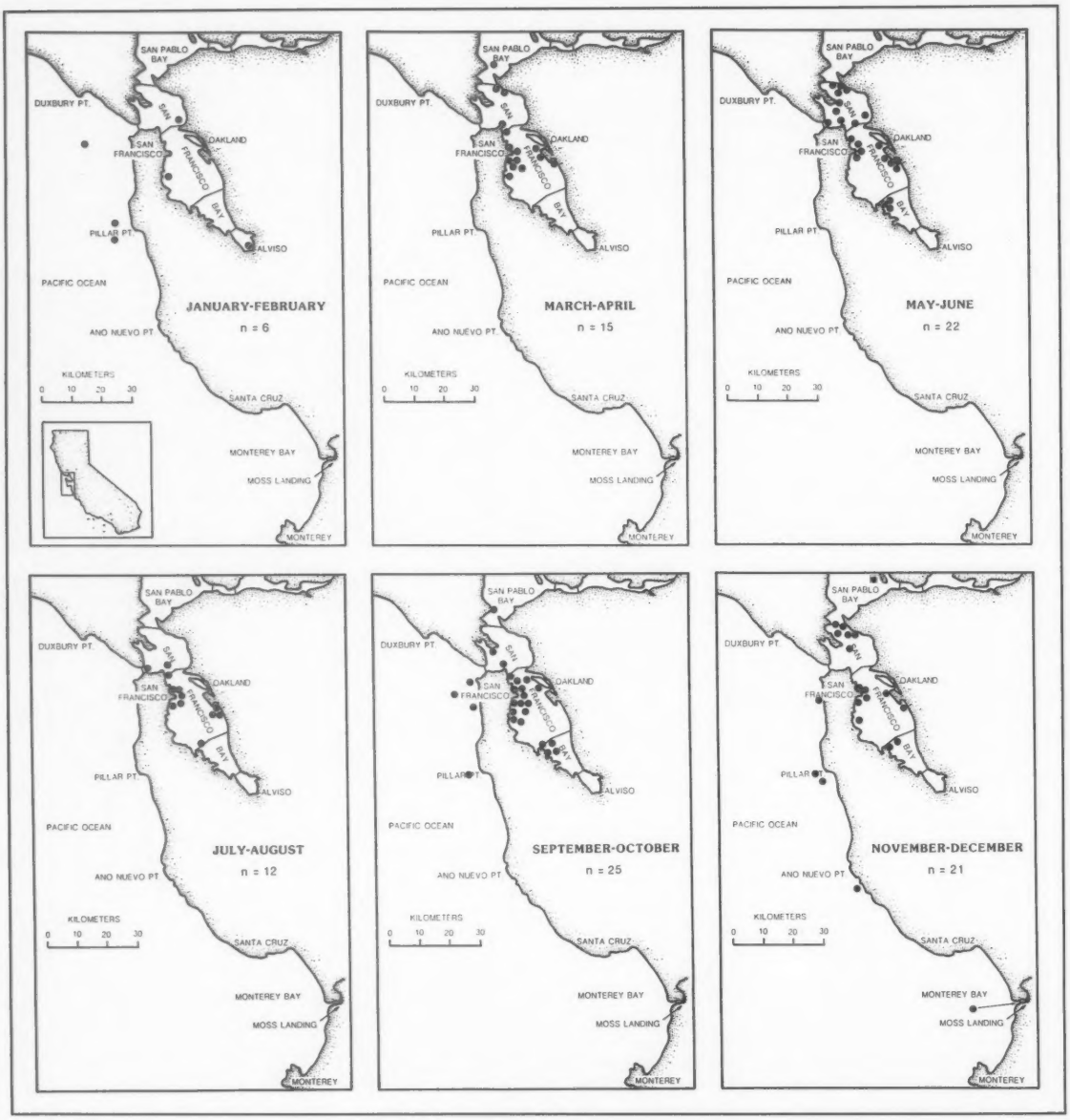

Figure 3

Bimonthly distribution of leopard shark recoveries in and around San Francisco Bay, California, 1979–88, for which recapture location and date were known.

Of the recoveries, 81.5% were reported by sport anglers, 12.0% by commercial fishermen, and 6.5% of the fish were found on shore or had an unknown recapture method. Those recovered by recreational anglers were rather evenly divided between shore and boat anglers, with skiff fishermen dominating the latter category. The important role of recreational anglers in the recovery of tagged fish appears to reemphasize the predominance of recreational users of the leopard shark resource.

Over the 9-year period, most fish were recaptured during the months of September (20%) and June (13%);

the fewest were returned in February (2%), January (4%), and July (5%). The return rate for 'healthy' fish was 9.9% and that of 'injured' fish, 15.8%. Clearly, there is no indication that handling during the tagging process induced excess tagging mortality. The sex ratio of recaptured fish was exactly the same as at tagging (53% males) indicating little if any selective mortality with regard to sex.

Movements

Bimonthly distribution patterns were plotted using recapture information from 101 recoveries made during 1979–88, for which recapture location and date were known (Fig. 3). From about March through August recoveries were restricted to the bay, while from September through February a marked pattern of dispersal occurred within and outside of the bay. One shark traveled as far as Elkhorn Slough near Monterey, about 140 km south of the entrance to San Francisco Bay.

To discern year-to-year differences in the temporal and general geographic pattern, Table 4 shows recoveries by year and recapture area (south San Francisco Bay, central and north bays, ocean/outside bay). The year 1983 was unique in that the greatest number of recoveries in any one year was made that year (22 fish, plus 2 fish recovered dead). It was also the only year that ocean recoveries were made as early as September, and the only year when an unusual number of recoveries (6 fish) was made in the central bay in June. (During the 9-year study period, there was only one other instance, in 1981, of a fish being taken in the central bay in June.)

No distribution pattern appeared to be correlated with fish size or sex, but due to the small sample size, the results do not preclude the possibility that the pattern may vary with sexual maturity or age. The sex ratio of fish taken in the ocean was normal (1:1); however, one commercial fisherman, who caught 3 of the 12 tagged fish taken in the ocean, reported that all 3 were gillnetted from the same depression on the sea floor in Half Moon Bay (one taken 13 Nov. 82, the other two taken in 1986 on 20 Oct. and 17 Nov.), and all 3 were large females with developing embryos.

Table 4
Distribution of leopard shark tag recaptures in and around San Francisco Bay, California, by year and area of recapture for which date and recovery area are known.

	Area of recapture			
Calendar year of recapture	South bay	Central & north bays	Outside bay/ ocean	Totals
1979	10	2	1	13
1980	8	9	0	17
1981	11	1	1	13
1982	5	4	3	12
1983	9	9	4	22
1984	9	2	0	11
1985	2	2	0	4
1986	1	0	3	4
1987	2	0	0	2
1988	3	0	0	3
Total	60	29	12	101

Mortality rates and virtual population analysis

The oldest ages reported for this species are 24 years for a male of approximately 135 cm in length and 20 years for a 130-cm female (Kusher 1987, fig. 8). However, we arbitrarily decided to use a maximum age of 30 years in Hoenig's (1983) regression equation since there are records of fish larger (180 cm; Kato et al. 1967) than those that were aged; we also noted that the largest female aged by Kusher (140 cm) was, at 18 years, not the oldest. Because the largest fish cited above was taken prior to the time when there was more than nominal fishing directed at this species, we feel that M may be assumed approximately equal to the Z from Hoenig's regression equation. The result of taking $t_{max} = 30$ in the equation was an estimated M of 0.14.

While we have no explicit estimate of a tag-shedding rate from this experiment, the results of Kato and Carvallo (1967) from multiple tagging of sharks at the Revillagigedo Islands, Mexico, indicated a minimal annual shedding rate of 0.095. We have taken this value, converted it to an annual instantaneous loss rate of 0.10, and added it to the previously estimated 0.14 to obtain $X = M + 0.1 = 0.24$ for use in lieu of natural mortality in the VPA. We assume, and believe it reasonable given the apparent hardiness of the animals and toughness of their skin, that there was no instantaneous (type I) tag shedding.

With regard to the percent of tag recoveries reported to us, we again have no "built-in" estimate, but the California Department of Fish and Game has conducted extensive studies on the return rates for various reward levels associated with tagged striped bass in the same general area that the leopard shark tagging occurred (Stevens et al. 1985). Based on their experience (D. Kohlhorst, Calif. Dep. Fish Game, Stockton, CA 95205, pers. commun., Nov. 1988), it seemed that a 50% reporting rate would be the best value to use as an adjustment for tag recoveries in this case. To utilize this adjustment in the VPA, we use half the actual number of tag releases as the target for convergence.

Table 5

Leopard shark tag recoveries in and around San Francisco Bay, California, including natural mortality (M), estimated fishing mortality (F), and rate of exploitation (E), by post-tagging annual time intervals.

Time interval	Recovery period	Tags recovered	Assumed $M + 0.1$	F	E
1	10/1/79–9/30/80	25	0.24	0.061	0.055
2	10/1/80–9/30/81	18	0.24	0.059	0.054
3	10/1/81–9/30/82	12	0.24	0.053	0.048
4	10/1/82–9/30/83	26	0.24	0.163	0.141
5	10/1/83–9/30/84	13	0.24	0.119	0.105
6	10/1/84–9/30/85	3	0.24	0.038	0.035
7	10/1/85–9/30/86	3	0.24	0.050	0.046
8	10/1/86–9/30/87	5	0.24	0.116	0.103
9	10/1/87–9/30/88	3	0.24	0.099	0.088
	Total	108	$\bar{F} = 0.084$		

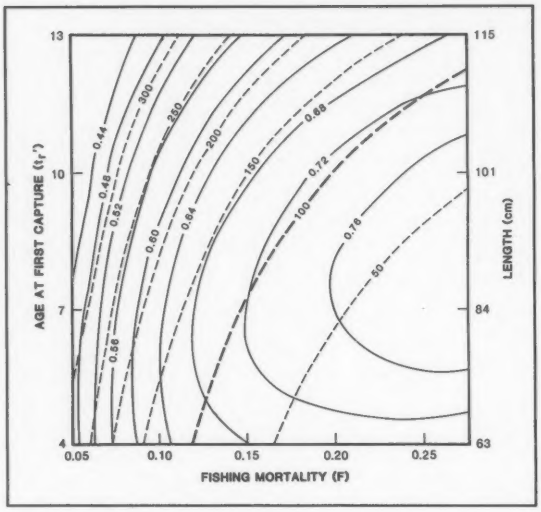

Figure 4

Isopleths showing percent population replacement of leopard sharks tagged in San Francisco Bay, California, in numbers (dashed lines) and yield per recruit in kilograms (solid lines), for $M = 0.28$ during the first year of life and 0.14 thereafter.

Tag recoveries by yearly intervals after the release period, estimated annual instantaneous fishing and natural mortality coefficients, and rates of exploitation are shown in Table 5. Note that these are all of the tag recoveries which could be assigned to the time intervals; other tabulations of recoveries in this paper may differ because of various missing information components.

Yield and stock replacement per recruit

Shown in Figure 4 is the yield-per-recruit isopleth diagram for $M = 0.28$ during the first year of life and 0.14 thereafter. Age at first capture ranges from 4 to 13 years, and F runs from 0.05 to 0.28. The graph indicates a fairly flat yield contour between $F = 0.15$ and $F = 0.28$, with age at first capture between 5 and 10 years.

Also in Figure 4 are isopleths showing percent population replacement per recruit over the same parameters used for the yield computations. For use in calculating population replacement, the fitted curve (Fig. 5) relating Ackerman's data on number of embryos to parental weight was

$$P_t = 22.64 - (7592)\,(0.4208)^{w(t)},$$

where P_t is number of embryos, $w(t)$ is maternal weight (kg) at age t, and the standard error of estimate equals 0.38313. The value for $w(t)$ was obtained from

$$w(t) = 0.00000305 \times \{172.4[1 - \exp(-0.0717[t + 2.302])]\}^{3.05}.$$

Replacement increases steadily as F tends toward 0 and age at first capture increases (equation 2). The shape of this surface is not unexpected, but clearly some type of density-related compensation would be needed to increase mortality or reduce fecundity as the population increases; otherwise in the absence of fishing the sea would be filled with leopard sharks. This mechanism might be in the form of higher juvenile mortality, less frequent litter bearing, or reduced average litter size. Holden (1973, 1977) discusses some possible mechanisms of this type and cites examples from the literature of marine mammals and elasmobranchs. We do not have information to examine any of these possibilities in the present case.

Discussion

If it is assumed that the tagged population approximates the real population, these results suggest that San Francisco Bay leopard sharks are mostly resident, with some moving out of the bay during fall and winter. Judging from the single Moss Landing recovery, limited population exchange evidently occurs between Elkhorn Slough and San Francisco Bay leopard sharks. Also, previously undocumented evidence was received during the course of this study from L. Talent (Oklahoma State Univ., Stillwater, OK 74078, pers. commun., July

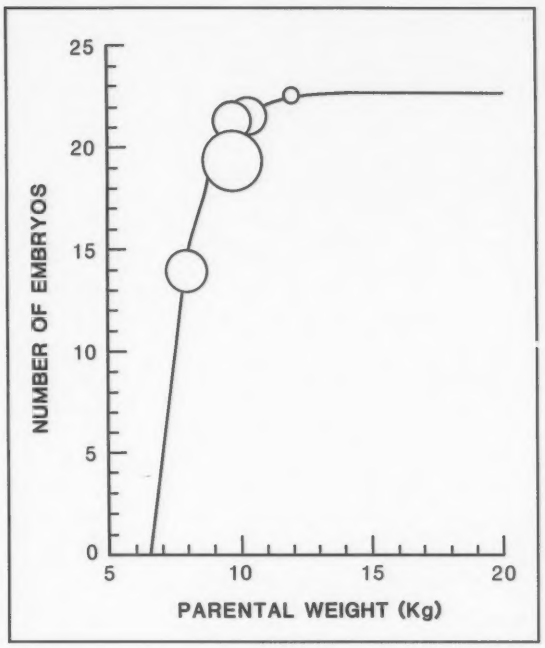

Figure 5

Fitted monomolecular curve relating mean number of leopard shark embryos in litters to parental weight. Areas of symbols are proportional to weighting factors of points used in the fitting process.

1982), who reported that a leopard shark tagged by him in December 1971 in Elkhorn Slough, Moss Landing, California, was recaptured February 1973 in south San Francisco Bay.

It is not known to what extent fishing effort influenced the recapture pattern, because effort information on the commercial and recreational catch is not available to the degree of geographic precision needed for such an analysis. We do know that leopard sharks are susceptible to bottom fishing gear, whether it be baited hook, gillnet, or, to a lesser extent, bottom trawl. Judging from the available data on recreational and commercial landings, and the much greater proportion of recreational versus commercial tag recaptures, recreational anglers are the primary users of the leopard shark resource in northern California. Angling for bottom fishes takes place in most areas inside the bay system year-round (Squire and Smith 1977), although in winter, inclement weather may lower fishing effort within the bay as well as along the open coast. Bottom-fishing effort in the ocean is thought to be comparatively less than in the Bay at least in waters shallower than 91 meters, the reported depth range of this species.

The 1983 peak in the tagged fish recovery rate and the associated rise in fishing mortality that we calculated (Tables 4 and 5) was unexpected. We have no evidence that fishing effort increased that year to cause this jump in the tag return rate, but there was a substantial rise in the California commercial catch of leopard shark that year, primarily driven by an increase in San Francisco landings (Table 1). There was also a similar rise in the estimated recreational catch (Table 2). The year 1983 was also one of unusual oceanographic conditions, when warm, nutrient-poor El Niño water intruded along the central California coast (McClain 1983, Norton et al. 1985). These El Niño conditions may have caused an influx of sharks from more southerly populations, but the increased rate of recovery for San Francisco Bay tagged fish should be independent of immigration of fish from other areas.

The California Department of Fish and Game (1987) and Pearson (1989), conducting trawl surveys of San Francisco Bay fishes, have observed higher trawl catches of leopard sharks during wet as opposed to dry years, and 1983 was indeed a wet year. That year the bay system experienced the highest delta outflows from the Sacramento-San Joaquin River systems in over 10 years, and June freshwater outflows were twice that of the previous wet year of 1982 and six times the previous decade's average outflow for that month (Calif. Dep. Water Resour., DAYFLOW Prog. Summ., Sacramento, CA 95816, Sept. 1987). Perhaps the anomalous conditions affected the local distribution and availability of central California leopard sharks and possibly their benthic prey, making the sharks more vulnerable to centers of fishing pressure.

In estimating the mortality, yield, and stock-replacement values, it was neccessary to make many assumptions and adjustments. Clearly we must assume that the tagged fish rapidly mix with the balance of a relatively closed San Francisco Bay population, and that tagged and untagged animals are equally likely to be caught. But because of the paucity of this type of information on these animals, an apparent high susceptibility of elasmobranch stocks to fishing pressure, and the noticeable increase in fisheries targeting on sharks, we felt it appropriate to present our best estimates based on the available data and current knowledge of elasmobranch biology.

In the case of the leopard shark, high stock maintenance is surely more important than a large yield per recruit. And while there is obviously something wrong with the stock replacement values which exceed 100% on an equilibrium basis, we would like to accept the 100% isopleth as reasonably valid. Noting in Table 5 that estimated F's ranged from 0.038 to 0.163 with a mean of 0.084, and observing in Figure 4 that the 100% replacement isopleth runs well to the right of the

0.68-kg isopleth over the higher observed levels of fishing mortality, it appears that management for full stock replacement would not involve a very great loss of yield per recruit. In fact, assuming an F of 0.2 and an age of first capture of 10 years, which equates to a 100-cm (40-inch) size limit, yield per recruit is less than 10% below the maximum shown in Figure 4. And given any F between the mean estimated value of 0.084 and the maximum estimate of F, the yield with the 100-cm size limit is within 10% of the maximum for that F.

However, in terms of numbers caught per recruit there is a substantial decline as the size limit increases. At $F = 0.2$, numbers per recruit values are 0.126, 0.192, and 0.292 for size limits of 100, 84, and 63 cm respectively; corresponding mean weights of fish comprising the retained catch are 5.8, 4.0, and 2.4 kg. All of these estimates assume that mortalities due to hooking and releasing undersized fish are negligible.

Based on the above information, a viable management strategy for the leopard shark would appear to be a size limit of 40 inches (100 cm). Although this size limit results in a 34% decline in numbers caught compared with a 33-inch (84 cm) limit, the fish which can be kept are almost 50% larger. Further, stock replacement is at the 100% level as compared with only 55% at the smaller size limit.

We stress, however, that our mortality and fecundity estimates were based on data from studies in only one area within the animal's geographic range, and the extent to which these can be extrapolated to the entire coastal population is not known.

Acknowledgments

We wish to thank David Holts, Mark Helvey, and Nancy Lo for reviewing the manuscript and making useful suggestions, and we are especially grateful to Patrick Tomlinson for pointing out a number of errors and omissions in his review of the manuscript and for providing a very insightful discussion of the contents. Also, we are indebted to an anonymous reviewer for detecting an important quantitative error. We would also like to thank Susumu Kato for providing valuable advice during all phases of the tagging project, and to others who helped tag and recover the fish. John Witzig and Joyce Underhill generously supplied leopard shark catch data, and Lorraine Prescott provided editorial assistance.

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Evidence of Survival Value Related to Burying Behavior in Queen Conch *Strombus gigas*

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Interest in queen conch *Strombus gigas* aquaculture and more efficient management of fished stocks has increased due to the declining catches of this species throughout its range (Brownell and Stevely 1981). Knowledge of conch survival is critical to the success of extensive and intensive aquaculture, and also to management of the exploited stocks. Information on survival, including predation rates during the period after larval conch have left the planktonic (drifting) stage and settled onto the bottom until the time they emerge and graze about on the bottom, is very limited.

Despite field searches conducted by numerous researchers in different areas, very few small conch (<1 year-old; ~5 cm in length) have been found in nature (Robertson 1959, Randall 1964, Hesse 1979, Davis and Hesse 1983). Research by Iversen et al. (1986) in the Berry Islands (Bahamas) using a variety of devices to sample the substrate and the substrate-water interface confirmed the paucity of young conch on or near the substrate surface in areas adjacent to aggregations of >1-year-old juveniles. It seems reasonable that these very young conch do not migrate over long distances to the cays where we find the large juveniles, but are carried during their planktonic life by currents to these locations. These findings suggest that conch may be buried almost continuously until they reach a shell length of ~5 cm.

The purpose of this study is to use tag-recapture data to examine the relationship between survival of juvenile conch and their burying activity.

Methods and materials

The data used in this study were collected in the Berry Islands (Bahamas) about 190 km east of Miami, Florida (Fig. 1). A wide range of conch sizes (3.5–22.0 cm) was tagged during these experiments at all seasons and at several different cays to account for the effects of different habitats, conch sizes, and seasonal variation.

The sampling area, consisting of shallow sand flats with abundant turtle grass *Thalassia testudinum*, is described in more detail by Iversen et al. (1987).

Individual conch were tagged with thin, numbered plastic tags affixed to the spire with underwater epoxy. Shell length was taken using a measuring board (Iversen et al. 1987). Shallow intertidal waters were sampled by wading and the deeper offshore water by snorkeling. Counts of tagged conch were made on 23 sampling trips lasting 4–5 days made approximately every 5 weeks between May 1980 and February 1983. A conch was considered to be buried when it was not found on one or more sampling trips, but was found alive on subsequent visits (Table 1). We believe this to be a reasonable assumption, because the aggregations of conch we studied remained in close proximity to the cays and when not buried were easily located. Conchs as large as 10–15 cm in length which we placed in 25-m^2 pens would bury and were not found on some visits despite intensive searching. On subsequent visits a month or more later, they would reappear on the surface of the substrate. For example, of 27 tagged conch in one pen, seven were buried on at least one visit between April and December 1980. Tagged individuals released at various cays that were not subsequently found were considered to have fallen prey to predators; large juveniles ($\gtrsim$16 cm) were assumed to have migrated offshore to deep water (Iversen et al. 1987).

Results

Our tagging data show a significant positive correlation (Fig. 2) between survival and percent buried for conch released in the subtidal region of about–2 m depth south of Vigilant Cay (shell length range, SLR, 3.5–16.5 cm; $r = 0.80$; $P<0.01$), and for conch from intertidal zones at Cat Cay (SLR 4.5–18.0 cm; $r = 0.56$; $P<0.05$) and Little Cockroach Cay (SLR 8.0–22.0 cm; $r = 0.81$; $P<0.05$).

Discussion

Predation is probably the most important cause of natural mortality on stocks of >1-year-old juvenile conch. Based on our searches for parasites in juveniles and adult conch, and our field observations, we do not believe that parasites or diseases play an important role in conch survival. There are reports of isolated mass mortalities of conch

Manuscript accepted 28 December 1989.
Fishery Bulletin, U.S. 88:383–387.

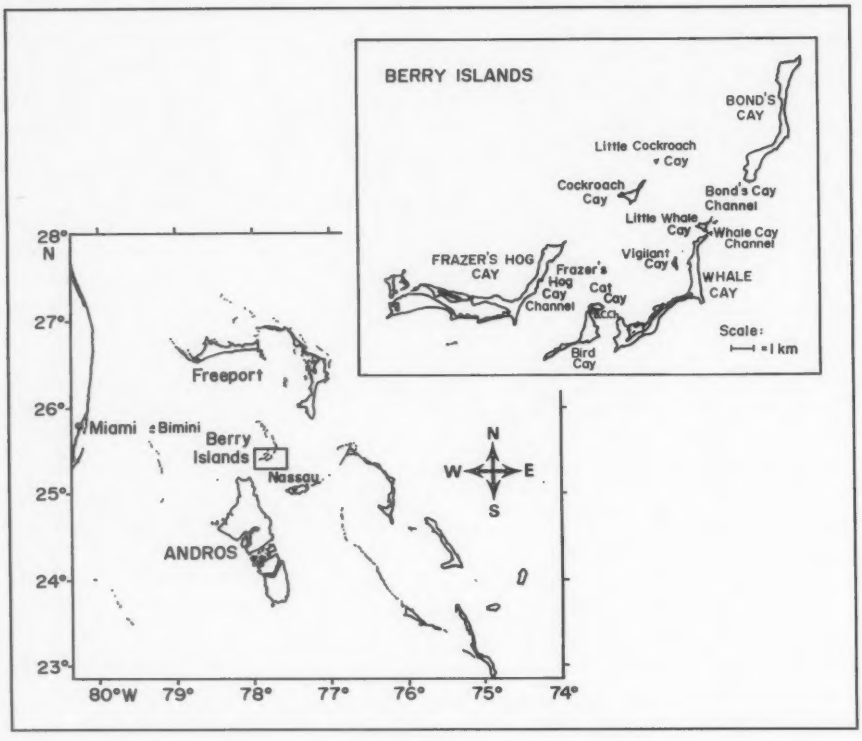

Figure 1
Location of *Strombus gigas* study site in the Berry Island (from Iversen et al. 1987).

Table 1
Example of database used in this study of queen conch burying behavior. Tagging location: Little Cockroach Cay, Berry Islands, Bahamas. Tagging date: 27 May 1980.

	Field observations								
	1980							1981	
Tag no.	05/27	06/23	08/21	09/05	10/03	11/01	12/16	01/23	03/03
0617	14.9	15.3	16.0	(B)	(B)	17.6			
0618	15.8	(B)	(B)	(B)	(B)	(B)	(B)	18.6	
0619	16.5	16.8	17.6						
0620	15.2	15.7	16.6	(B)	17.8				
0621	17.1	(B)	18.1	18.6	19.0				
0622	15.1	15.7	16.6	17.2	(B)	17.7			
0623	16.2	(B)	17.4	17.7	(B)	18.8			
0624	16.7	17.3							
0625	14.7	15.6	16.2	17.0	17.1				
0626	14.4	15.1	15.9	16.4	16.8				
0627	15.2	16.0	16.5	17.4	(B)	18.1			
0628	14.1	(B)	15.3	(B)	16.1	16.0			

A tagged conch is considered to be buried (B) if not found on one or more subsequent trips, but is eventually found. It is assumed to have been killed or to have migrated offshore if not subsequently found. No tags from this group (0617–0628) were found in the vicinity of Little Cockroach Cay during the period February 1981 to the end of the study, February 1983, despite 11 field searches made every 4–6 weeks during this period. Conch of about 18–20 cm shell length generally migrate into deep offshore waters from this cay (Iversen et al. 1987).

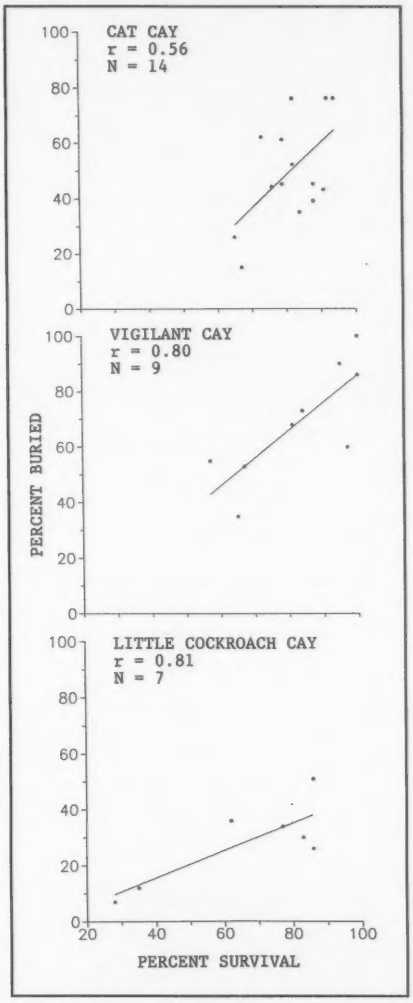

Figure 2

Relationship between *Strongus gigas* burying activity and survival. Vigilant Cay: offshore, 171 conch tagged 3 October 1980; SLR 6.7–9.3 cm. Cat Cay: 455 conch tagged 27 May 1980; SLR 8.9–19.1 cm. Little Cockroach Cay: 84 conch tagged 8 April 1981; SLR 9.2–15.5 cm. N = number of months the experiment lasted.

during the summer on tide flats when temperatures reached extremely high levels (Weil and Laughlin 1984).

In the few trials made to date, survival of hatchery-reared small conch (2.0–7.0 cm in length) released in different locations in the Bahamas and the Caribbean has been extremely low. For example, in St. Croix, Coulston et al. (1987) reported that unprotected juvenile conch did not survive. And in a small-scale preliminary trial, Iversen et al. (1986) reported complete mortality of 1.3–3.7 cm long, hatchery-reared conch placed under protective screens laid on the substrate and held in place by rocks.

To fully interpret our results and put them in context with what is known about mortality and predation in juvenile queen conch, it is necessary to consider the factors affecting both burying behavior and mortality/predation. Concerning the former, we first note that very small conch are almost never found unburied. Although emphasis of our research was on animals larger than 5 cm in length, we searched for small conch during all field trips. Of the 491 small conch (1–9 cm) we found, all but a few (~3%; $N = 15$) were buried, some as deep as 20 cm, while others were barely covered by broken shells and rubble in shallow depressions on a large tidal flat. With only a few exceptions, those found on the substrate were larger than ~5 cm.

Iversen et al. (1987) showed significant differences in burying activity within a tidal cycle at various sites in the Berry Islands. Significantly more conch buried on high tides than on low tides, which they suggested may be a response to possible increased predator activity during high tides when large swimming predators can reach the upper intertidal zone. This apparent tidal-height behavioral response should not be triggered in the deeper (subtidal) water offshore of Vigilant Cay where we released tagged conch. Our results showing a relationship between survival and burying behavior suggest that conch over a wide range of sizes are less vulnerable to predation when buried. This may explain why the highly vulnerable, thin-shelled young-of-year bury for extended periods.

In addition to the effects of conch size and tide stage, burying behavior may be affected by time of year (a proxy which encompasses a number of environmental circumstances, such as water temperature and wind and sea conditions). According to Hesse (1979), seasonal variation in burying behavior is also a factor, with more active burying during the winter when the waters are cooler and the winds stronger than during the remainder of the year. However, no clear-cut seasonal trend in burying activity is evident from our data. Rather, there are generally wide variations in the number of animals buried, which we believe are possibly related to different environmental conditions in the different habitats of the cays where we collected our data. Our size-frequency data suggest that burying activity is not related to the size of the animals, after they attain a shell length of ~5–6 cm.

With respect to mortality, Appeldoorn (1985) showed that juvenile queen conch mortality rates were highest during summer and lowest during winter in Puerto

Rico. Jory and Iversen (1983) found in their studies in the Berry Islands that the highest levels of predation occurred during the summer and the lowest during the winter. They also suggested that reduced mortality in the winter may be due to reduced predator activity and a decrease in conch activity.

Small conch do not grow in length during the winter period of burying (Appeldoorn 1985, Iversen et al. 1986). Therefore, when they emerge in the spring to begin active foraging on the substrate they would have gained no obvious "size" survival advantage as a result of their "hibernation." Johnson et al. (1964) demonstrated that the shell thickness of queen conch increases with activity, and because buried conch would not be expected to be very active during the winter, shell thickness would probably not increase substantially over this time.

Conch survival estimates show trends common to many mollusks: low survival for small animals, increasing as the size of the mollusk increases (Jory et al. 1984; Appeldoorn 1984, 1988; Iversen et al. 1986). Recoveries from 259 tagged wild conchs (SLR 5.0–21.0 cm) at Little Whale Cay, Bahamas, over a 6-month period showed a significant positive correlation between length at tagging and percent recovered ($r = 0.95$; $p<0.05$). This correlation suggests that within this size range mortality decreased with increased conch size. Using floating cages to provide protection from predators and increase survival, we demonstrated that as high as 96% survival was achieved for conch in the size range 5.0–8.0 cm over a 1-year period, while survival of tagged non-caged small conch of similar size after 6 months was only between 0 and 10%. Similar evidence on differential survival by conch size was gathered in Puerto Rico by Appeldoorn (1984) who, by using short-term (~8 weeks) mark-recapture data for both queen conch and milk conch (*S. costatus*), determined that larger individuals suffered less mortality than smaller ones. Jory and Iversen (1988) provided direct evidence of a lack of increase in shell thickness in small juveniles by examining the relationship between shell breaking strength and shell size of queen conch. They found little increase in breaking strength up to a size of ~5.5 cm, suggesting that queen conch shells are relatively thin below this length. Above ~5.5 cm, pressure to crush shells increased rapidly with increasing shell length.

As queen conch increase in size, their spines increase in length and become more robust. Spines may reduce predation on mollusks in various ways (Palmer 1979). They increase the overall size of the shell, thereby limiting predation to larger predators. Conch spines also distribute crushing pressure over a greater area of the shell, thus increasing the pressure required to crush the shell (Jory and Iversen 1988). Spines also serve as additional area for attachment of epibionts which may help conceal mollusks from predators (Feifarek 1987).

The amount of attached organisms on the shells of conch increases with the size of the conch, suggesting a decrease in long-term burying activity with increase in conch size (Iversen et al. 1986). All of the smallest conch we collected had very clean shells with no growth of attached organisms, in contrast to the rapid and heavy growth of algae we observed on the shells of similar-sized conch in hatchery tanks at the University of Miami laboratory and in floating cages at Little Whale Cay, Bahamas. These results further support the hypothesis that young conch spend most of their early life (up to ~1 year of age) below the surface of the substrate, a strategy that may provide haven from some predators (Hesse 1979, Appeldoorn 1985, Iversen et al. 1986).

The relationships between shell size and strength and between survival and burying have practical application in suggesting place and time of year to release hatchery-reared conchs, in order to both minimize predation and increase the efficiency of planting programs using hatchery-reared juveniles of queen conch and several other mollusk species. Placement of young hatchery-reared conch in relatively safe, natural areas optimal for burying and with certain physical characteristics such as strong currents, fine-to-coarse sand, and abundant intact and broken mollusc shells, where red and green algae and sponges occur (as described in Iversen et al. 1986) would obviate the need for overwintering in an expensive hatchery facility. Further, as suggested by Jory and Iversen (1983), fall planting of small hatchery-reared conch would provide time for them to acclimate to their environment before the spring or early summer "emergence." This is particularly relevant in view of evidence available for other mollusk species, where hatchery-reared juveniles are more vulnerable to predators when released in nature than wild juveniles (Tegner and Butler 1985). Development of an inexpensive enclosure for holding large numbers of young-of-the year under the surface of the substrate could further increase survival of hatchery-reared conch juveniles.

Acknowledgments

This research was funded jointly through the University of Miami by the Wallace Groves Aquaculture Foundation and the Kirby Foundation. This support is deeply appreciated as is the field assistance provided by many individuals. Employees on Little Whale Cay gave generously of their time and knowledge of the area.

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Stomach Contents and Parasite Infestation of School Bluefin Tuna *Thunnus thynnus* Collected from the Middle Atlantic Bight, Virginia*

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In the western Atlantic Ocean, northern bluefin tuna *Thunnus thynnus* are distributed from Labrador and Newfoundland to the Gulf of Mexico, Caribbean Sea, and off Venezuela and Brazil. The northern bluefin tuna is epipelagic and usually oceanic, but seasonally strays near the coast (Collette and Nauen 1983). During June through October, these tuna are common off the eastern United States and Canada (Squire 1962) and support both commercial and recreational fisheries. From the end of May to August, many pods of small school bluefin tuna (<100 kg) migrate past Virginia on their way to more northern feeding grounds. These tuna are caught 30 to 60 km off the Virginia coast in the vicinity of numerous shoals or "hills," by recreational anglers trolling dead bait or lures on or near the surface (Figley 1984). In 1986, 886 boats participated with some degree of regularity in the recreational fishery for tuna and billfish out of Virginia ports (Bochenek and Lucy In press). Further north, there is a recreational fishery for giant (>200 kg) and medium (100–200 kg) bluefin tuna, and, to a lesser extent, school bluefin tuna (Figley 1984).

Bluefin tuna are opportunistic predators that prey upon fishes, mollusks, crustaceans, and salps (Crane 1936; Bigelow and Schroeder 1953; Krumholz 1959; Dragovich 1969, 1970; Mason 1976; Matthews et al. 1977; Holliday 1978). Pacific bluefin tuna *Thunnus thynnus orientalis* caught off California and Baja California preferred the same prey as the Atlantic Ocean subspecies *Thunnus thynnus thynnus* (Pinkas 1971).

The spawning stock of the western Atlantic bluefin tuna has declined sharply since 1970, and both recruitment and juvenile stock size are still substantially lower than in 1970 (ICCAT 1987). Thus, information about life-history characteristics, such as trophic habits, is essential for developing sound management plans for this important commercial and recreational fish. Mason (1976) and Holliday (1978) studied the feeding behavior of school bluefin tuna captured along the eastern coast of the United States; however, only 68 bluefin tuna stomachs were collectively examined from fish caught off or near the Virginia coast (lat 36–38°N and long. 75°W). Therefore, knowledge of the feeding habits of school bluefin tuna off the Virginia coast is relatively sparse. The present paper describes the findings of stomach content analysis for juvenile bluefin tuna collected during the summer of 1986 by recreational fishermen along the mid-Atlantic coast off Virginia.

Methods and materials

During June and July 1986, stomach samples of 97 bluefin tuna were obtained from recreational fishermen as they landed their catch at Rudee Inlet, Virginia Beach, and at Wachapreague on the eastern shore of Virginia. Curved fork length (mm) and the area of capture (Fig. 1) were recorded for each fish. Fish that could not be identified with a specific area of capture were eliminated from the sample. Weights (kg) were recorded for tuna officially weighed on certified marina scales. Stomachs were removed and placed in 10% buffered formalin. Stomachs were opened and designated in the laboratory as either containing food or empty. Stomachs containing only parasites were classified as empty. Stomach contents were rinsed in water and stored in 10% ethanol until identification.

Prey items were sorted into major food groups (fishes, crustaceans, mollusks, and unidentifiable remains), enumerated, and identified to the lowest possible taxon with the aid of a binocular dissecting scope. Volumes were determined by water displacement using a graduated cylinder and measured to the nearest 0.5 mL. Fishes too far digested for certain identification were placed in an unidentified teleost category and used in estimating total prey volume. The majority of unidentified teleost material resembled remnants of sand lance (*Ammodytes* spp.) more than any other recognizable species.

*Contribution no. 1580 of the Virginia Institute of Marine Science.

Manuscript accepted 18 December 1989.
Fishery Bulletin, U.S. 88:389–395.

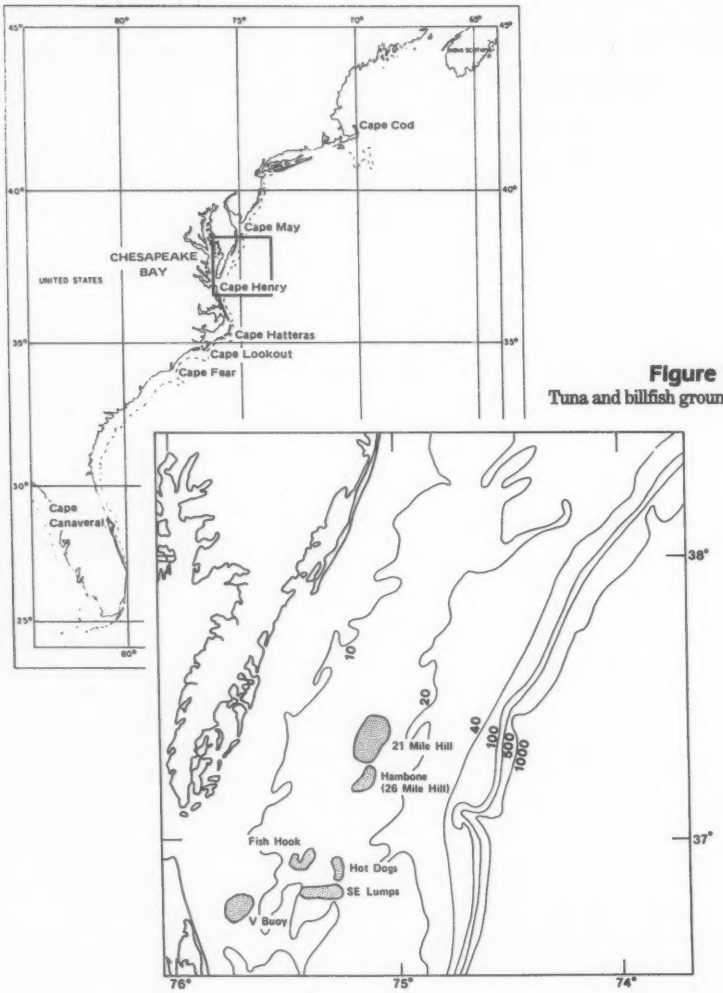

Figure 1
Tuna and billfish grounds off Virginia.

To help evaluate the relationship of the various food items found in stomachs we employed an index of relative importance (*IRI*) (Pinkas 1971):

$$IRI = (N + V)\,F,$$

where N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage. Percent *IRI* consisted of the *IRI* value of each prey category (unidentified fish and cephalopods excluded) divided by the sum of the *IRI* values (unidentified fish and cephalopods excluded). To determine if the quantity of the key trophic group differed by area of capture (Fig. 1), displacement volume was compared against three areas sampled with a one-way ANOVA model (with displacement volume as the dependent variable and area of capture as the independent factor). The key trophic group was composed of pooled volumetric contributions of both identified and unidentified teleost remains. The three areas were: (1) the "Hot Dog," (2) "'Fish hook" and "S.E. Lumps," and (3) "21 Mile Hill." The "Fish hook" and "S.E. Lumps" areas were pooled because boat captains generally fished both areas during the same trip. The remaining areas, "26 Mile Hill" and "V-Buoy," were both eliminated from the hypothesis test because of low sample sizes ($N = 2$ for both). Significant differences were contrasted by a Student-Neuman-Kuels (SNK) multiple range test set at an experiment-wise error rate (EWER) of 0.05 (Zar 1984). Tests for normality and equality of variance (Zar 1984)

Table 1

List of prey species or class groups occurring in stomachs of juvenile bluefin tuna *Thunnus thynnus* from the Mid-Atlantic Bight, Virginia, 1986.

	No. of individual prey items from 72 stomachs	Percent by number	Volume (mL)	Percent volume	% Frequency of occurrence based on stomachs containing food ($N = 72$)	Index of relative importance (*IRI*)	% *IRI*
Teleosts							
Ammodytes spp. (sand lance)	403	84.1	1028.0	30.75	48.6	5583.2	0.968
Peprilus triacanthus (butterfish)	11	2.3	84.0	2.51	2.8	13.5	0.002
Hippocampus erectus (lined seashore)	9	1.9	2.5	0.07	1.4	2.7	0.0004
Aluterus scriptus (scrawled filefish)	1	0.2	1.5	0.04	1.4	0.4	0.00006
Unidentified teleosts (primarily sand lance)	NA	NA	1653.5	49.46	75.0	NA	NA
Cephalopods							
Lolliguncula brevis (Atlantic brief squid)	48	10.0	432.0	12.92	6.9	158.3	0.027
Loligo pealeii (longfin squid)	2	0.4	124.0	3.71	2.8	11.6	0.002
Unidentified cephalopods	NA	NA	5.0	0.15	1.4	NA	NA
Miscellaneous							
Salpidae			12.3	0.37	8.3	NA	NA
Idotea sp. (Isopod)	5	1.0	0.5	0.01	1.4	1.5	0.0002
Totals	479		3343.3			5771.0	1.0
Total stomachs analyzed	97						
No. (%) containing food materials (identified and unidentified)	72(74.2)						
No. (%) empty	25(25.8)						

indicated that the logarithmically transformed volumes were appropriate for ANOVA.

Results

Food analysis

Of the 97 juvenile bluefin tuna stomachs examined, 72 (74%) contained food. These tuna averaged 21.3 kg ($n = 7$, SD 7.7, range 15–39 kg) with a mean fork length of 90 cm ($n = 85$, SD 13, range 70–132 cm). Stomach contents consisted of two primary food groups: teleosts and cephalopods. Teleosts contributed over five times the percent volume to the diet (82.8%) compared with cephalopods (16.8%) (Table 1). Teleosts occurred in 91% of those stomachs containing food items and accounted for 86% of the total identified prey items (Table 1). Major subgroups of identifiable teleosts by percent frequency of occurrence (based on number of stomachs containing food), *IRI*, and percent *IRI*, listed in decreasing order were sand lance, butterfish *Peprilus triacanthus*, lined seahorse *Hippocampus erectus*, and scrawled filefish *Aluterus scriptus* (Table 1). Sand lance was the predominant teleost occurring in stomachs, especially considering that the unidentified teleost category (probably primarily sand lance) contributed the greatest volume of all prey species found (Table 1).

Cephalopods occurred in 14.4% of those stomachs containing food (Table 1). This group was represented by two species, the Atlantic brief squid *Lolliguncula brevis* and the longfin squid *Loligo pealeii*. Unidentified cephalopod remains accounted for the lowest percent volume (0.2%) of prey items in stomachs containing food, whereas Atlantic brief squid contributed the highest (12.9%) (Table 1).

A third, miscellaneous prey category included salps and one immature species of isopod. A cigarette wrapper and piece of *Sargassum* weed were each present in two of the stomachs.

The combined volumetric contributions of teleost remains to the gut were significantly affected by area of capture (ANOVA; $F = 8.93$, df 2, 82, $P < 0.0003$). Stomach contents of tuna landed from "21 Mile Hill" had significantly higher volumes of teleost remains than did stomachs taken from either the "Hot Dog"

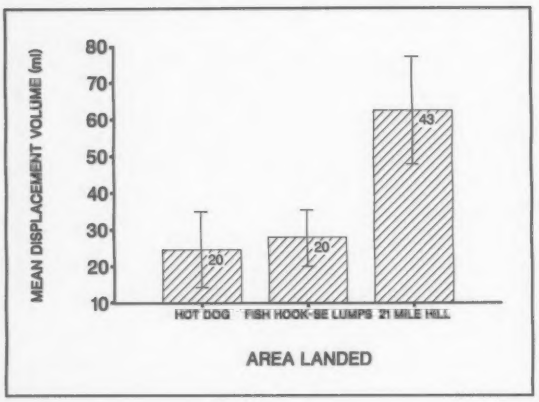

Figure 2

Mean combined displacement volume of identified and unidentified teleost remains from stomachs of bluefin tuna collected from three different areas off Virginia. Numbers within each bar indicate number of specimens sampled; vertical lines indicate ±1 SE.

or "Fish hook and S.E. Lumps" areas (SNK: EWER 0.05) (Fig. 2).

Digenetic trematodes *Hirudinella ventricosa* were found in 8 (11.1%) of the stomachs and averaged 10 mm in length and 2–3 mm in width. The worms were never attached to the lining of the stomach and were typically found at the posterior end. The number of worms per stomach ranged from 1 to 2 with a mean of 1.14 *H. ventricosa* per individual stomach. The possible effects of area landed on the number of trematodes occurring in the stomachs were not evaluated because of the relatively low rate of parasitism.

Discussion

Diet

This study indicates that school bluefin tuna, captured off the Virginia coast, feed predominantly on the sand lance. Mason (1976) was the first to report sand lance as a prey item of school bluefin tuna caught off the U.S. East Coast. He also reported sand lance to be the most important prey of school bluefin tuna caught off Virginia, but for fish taken north of Virginia, mackerel (*Scomber* spp.) replaced sand lance as the dominant prey. Holliday (1978) also found the sand lance to be the predominant food item for bluefin tuna captured by trolling along the U.S. East Coast. The *IRI* of sand lance in this study (*IRI* = 5583) is very similar to that reported by Holliday (1978) (*IRI* = 4896).

Sand lance form dense schools over New England and mid-Atlantic Continental Shelf areas. They occur throughout the water column during daylight hours, and are available to tuna predation at various depths (Meyer et al. 1979, Auster and Stewart 1986). Tuna predation on sand lance may affect the populations of this important forage species off Virginia. Reproducing populations of sand lance, as indicated by egg and larvae counts, exist on the Virginia shelf (Norcross et al. 1961); hence, the Virginia coast is an important habitat to the species. The sand lance serves as an important link between secondary producers and higher trophic-level fish and mammals in marine food chains (Bigelow and Schroeder 1953); thus, extensive predation by tuna could affect marine mammal populations. A cause-and-effect relationship may exist between low mackerel and herring stocks (resulting from heavy fishing mortality) and the observed population explosion of sand lance larvae in the mid- to late 1970s (Sherman et al. 1981); thus, tuna predation on sand lance could be beneficial to the return of mackerel and herring stock abundance.

The Atlantic brief squid was the second most important item consumed by school bluefin tuna examined in our study. Mason (1976) found two squid in the 20 fish he examined from Virginia waters. Holliday (1978) also reported similar species of cephalopods in stomach contents of the bluefin tuna taken off the U.S. East Coast. Krumholz (1959), working near the Bahamas, reported salps as the second most important food item. In the western North Atlantic, Dragovich (1970) noted molluscs (mainly cephalopods) as second in trophic importance. Similarly, Matthews et al. (1977) also reported cephalopods, pteropods, and heteropods as being the most frequent invertebrate forage group after fishes. For California bluefin tuna, the second most important food item was the California market squid *Loligo opalescens* or the pelagic swimming crab *Pleuroncodes planipes*, depending upon the area of capture (Pinkas 1971).

The butterfish, lined seahorse, and scrawled filefish were found in very few stomachs, being rare contributors to the diet of bluefin tuna in this study. These prey species demonstrate considerable diversity in their foraging locations, including nearsurface, mesopelagic, and demersal habitats. It is possible that the butterfish, lined seahorse, and scrawled filefish are associated with drifting *Sargassum* weed; thus, tuna may feed in part around drifting *Sargassum* communities. Other miscellaneous items found in the stomachs were salps, the isopod *Idotea* spp., a cigarette wrapper, and *Sargassum* weed. Holliday (1978) also reported the occurrence of *Idotea* spp. in stomachs of bluefin tuna caught trolling near *Sargassum* communities. He hypothesized that the isopod and *Sargassum* weed were accidently ingested by the tuna while pursuing other prey.

Parasites

The digenetic trematode *Hirudinella ventricosa* occurred in 11% of the stomachs examined in this study. Mason (1976) also found an annulated hemiurid trematode in 2% of the bluefin tuna stomachs he examined from the western Atlantic Ocean. The trematodes in Mason's (1976) study were found in both empty stomachs and stomachs which contained food. Crane (1936) reported *Distoma*-like worms in 25% of giant bluefin tuna stomachs he examined off Maine. *Hirudinella ventricosa* (= *marina*) occurred in 9% of school bluefin tuna and 48% of giant bluefin tuna stomachs collected from North Carolina to Massachusetts (Holliday 1978).

Giant trematodes of the genus *Hirudinella* frequently parasitize scombroid fishes (Nigrelli and Stunkard 1947, Nakamura and Yuen 1961, Watertor 1973, Manooch and Hogarth 1983). Adult parasites typically attach to the stomach lining and remain near the site of attachment throughout this life-stage (Manooch and Hogarth 1983). These digenetic endoparasites have complicated life cycles involving an alternation of generations and hosts; however, the life cycle of *Hirudinella* spp. is still unknown (Manooch and Hogarth 1983).

Attempts to evaluate the incidence of parasitism by size and sex of the host and by geographical area of collection have demonstrated mixed results (Nakamura and Yuen 1961, Manooch and Hogarth 1983). Nakamura and Yuen (1961) examined the occurrence of the parasite *H. ventricosa* (= *marina*) in the stomachs of skipjack tuna *Euthynnus pelamis* collected from Hawaii and off the Marquesas. They concluded that significant differences in the occurrence of trematodes collected from these two areas were attributable to time (year of collection) rather than area. Manooch and Hogarth (1983) reported distinct differences in the incidence of parasitism by *H. ventricosa* between wahoo *Acanthocybium solanderi* from the coast of Florida-South Florida and wahoo from the rest of the southeastern Atlantic. They suggested that this difference may reflect two subpopulations of wahoo along the southeastern U.S. coast: a northern population characterized by high incidence of trematodes, and a southern population with a much lower incidence.

Watertor (1973) examined 258 bluefin tuna captured off the East Coast of the United States (lat. 35–40°N; long. 65–75°W) and off the northeast coast of South America (lat. 0–18°N; long. 50–82°W). Of these, 51 were infected with *H. ventricosa* (= *marina*), nearly twice the infection rate noted in this study. There are two possible explanations for this difference. First, the parasites described by Watertor (1973) were pooled from both the eastern U.S. and northeastern South American samples. Inclusion of a South American group, with possibly a higher prevalence of parasitism, similar in nature to that described for wahoo by Manooch and Hogarth (1983), might have biased the values reported by Watertor (1973). Secondly, Watertor (1973) did not report the overall size ranges of bluefin tuna used in his study. Inclusion of giant bluefin tuna, with a higher prevalence of parasitism (see Crane 1936) may also contribute to apparent differences in levels of infection.

Area effects

Environmental factors such as temperature and oceanographic frontal zones have been shown to markedly influence the distribution, abundance and catchability of tunas (Murphy 1959, Uda 1973, Laurs and Lynn 1977, Rockford 1981, Sund et al. 1981, Laurs et al. 1984). Murphy (1959) suggested that the aggregation of albacore *Thunnus alalunga* in clear water on the oceanic side of fronts in nearshore areas may reflect an inability to efficiently capture large, mobile prey in turbid coastal waters. This same mechanism may help to explain the higher combined displacement volumes of sand lance and unidentified teleost remains in the stomachs of tuna taken from the "21 Mile Hill" compared with the "Hot Dog" or "Fishook and S.E. Lumps" areas (Fig. 2). Turbidity associated with effluent from Chesapeake Bay might have reduced the ability of bluefin tuna to detect mobile forage such as the sand lance and other teleosts. The effluent from the Chesapeake Bay appears in shelf waters as a lens of freshened water (with high concentrations of bay water constituents) extending offshore and towards the south as a part of the general shelf circulation (Ruzecki 1981). The three areas in question are directly offshore of the Chesapeake Bay mouth (Fig. 1). Differences in the diet of bluefin tuna have also been attributed to depth of capture, availability and type of food in a given area, time of day or year, spawning, atmospheric conditions, physiological conditions of predator fish, size of prey, and size of the bluefin tuna (Dragovich 1970).

We conclude that the sand lance is the most important forage of school bluefin tuna off the Virginia coast and suggest that this prey species, as well as teleosts in general, may become more vulnerable to tuna predation in areas least affected by the turbid waters of the Chesapeake Bay plume. In addition, the occurrence of the digenetic trematode *Hirudinella ventricosa* in a small but significant number of bluefin tuna off Virginia suggests that variation in infestation rates of this parasite might provide a mechanism to help distinguish among possible subpopulations of bluefin tuna occurring in the Western Atlantic.

Acknowledgments

We thank J. Lucy, N. Chartier, and B. Sweeney for assistance in field collections, and B. Cornett and M. Peterson, participants in the Governor's School for Marine Science of the Virginia Department of Education for help in collecting and processing tuna stomachs and in enumeration of food contents. Special thanks to J. Lucy for his helpful advice throughout the duration of this study. Helpful reviews of the manuscript were provided by J. Colvocoresses, J. Lucy, J. Musick, and two anonymous referees.

This work was supported by funds from the Virginia Institute of Marine Science Advisory Services Program and National Marine Fisheries Service Port Sampling Program for Large Pelagics, Northeast Fisheries Center. First authorship was determined by a coin toss.

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Horizontal and Vertical Movements of Pacific Blue Marlin Captured and Released Using Sportfishing Gear*

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Despite the commercial and recreational importance of Pacific blue marlin *Makaira nigricans*, little is known about their biology or behavior. This is due mainly to their large size and pelagic habitat and the difficulty in maintaining them in captivity or observing their behavior in the wild. However, two techniques are available to elucidate their movements: capturing and releasing marlin fitted with identification tags, and tracking of fish carrying ultrasonic transmitters.

The recovery of tagged marlin has enhanced our understanding of the long-term geographical range of individual fish and their minimum rates of travel (Squire 1974, Squire and Nielsen 1983, Bayliff and Holland 1986), and growing interest in the tag and release of marlin by sportfishermen should produce an increasingly precise picture of marlin movements. However, this technique cannot answer questions regarding the vertical movements of marlin, and questions remain concerning both the survival of tagged fish following the trauma of capture and the nature of their behavior immediately upon release.

Fine-scale observations of the horizontal and vertical movements of pelagic fish can be obtained for periods of up to a few days by tracking fish equipped with depth-sensitive ultrasonic transmitters (Holland et al. 1985, 1990; Bayliff and Holland 1986). For billfishes, this technique has been used to track swordfish *Xiphius gladius* (Carey and Robison 1981) and striped marlin *Tetrapturus audax* (Holts and Bedford In press). Similarly, Yuen et al. (1974) tracked Pacific blue marlin but used temperature-sensitive transmitters to monitor ambient water temperature from which depth was later calculated using bathythermograph data. However, this study heightened concerns about tagging mortality rates because three of the five tagged fish died soon after release.

Here we report on the movements of six Pacific blue marlin tracked in the waters around the Hawaiian Islands. Of particular interest were survivorship and behavior of the fish immediately upon release, their patterns of vertical movement, and their overall patterns of horizontal movement. To discern any common patterns of movement associated with one particular area of ocean, three fish were caught and tracked from one well-defined location on the Kona coast of Hawaii. For comparison, two other tracks were initiated several miles away along the same coast, and one marlin was tracked off the Waianae coast of Oahu.

Methods

The ultrasonic tracking techniques employed were identical to those used previously to track yellowfin tuna (Holland et al. 1985, 1990; Bayliff and Holland 1986). The transmitters used in the present study had a nominal life span of 3 days and a maximum working pressure of 500 psi (Vemco, Halifax County, Nova Scotia). The signal, encoding depth information by variable pulse interval, was recorded on audiotapes for later onshore plotting of vertical movements of the fish. Horizontal location was determined every 15 minutes (or more frequently when necessary) by using a combination of Loran-C, radar, visual, and bathymetric fixes. Water temperature was measured by expendable bathythermographs deployed approximately every 3 hours.

Aggregate depth and temperature distributions were calculated (with 10-m and 1°C bins, respectively) as percentages of the total track time spent at any particular depth or temperature. For temperature, the combined distributions of all fish were calculated as the percentage of time spent in the various temperature strata relative to the upper mixed layer.

Each transmitter was attached with a 10-cm length of 130-lb test monofilament to a stainless steel "arrowhead" ($\sim 2.75 \times 1.75 \times 0.1$ cm; Fig. 1) modified from the type

*Sea Grant Publication UNIHI-SEAGRANT JC-90-13.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted 5 March 1990.
Fishery Bulletin, U.S. 88:397–402.

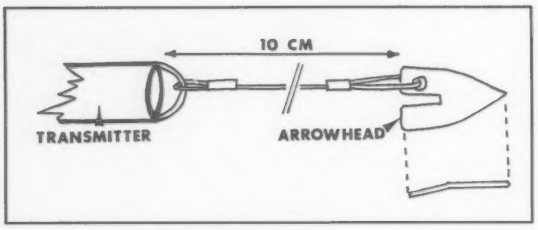

Figure 1
Tag attachment system for Pacific blue marlin. A stainless steel arrowhead, with downcurved tines and central notch to accommodate the prong of the applicator pole, is attached to the transmitter body with a 10-cm length of 130-lb test monofilament crimped in two places.

used by Yuen et al. (1974) and Carey and Robison (1981). The arrowhead fitted into the tip of a standard tagging pole to which the transmitter was loosely bound with rubber bands (Yuen et al. 1974, Holland and Bayliff 1986). The fish was harpooned in the trunk musculature, thereby allowing the transmitter to lie against the surface of the fish alongside the forward half of the dorsal fin. Once the transmitter was attached, the fish was released by cutting the leader, leaving the hook in place.

Fish were caught by surface trolling with artificial lures and standard sportfishing rods and reels. Two of the fish were caught on the tracking research vessel *Kaahele'ale*, and four were caught by teams participating in the 1988 and 1989 Hawaii International Billfish Tournaments (HIBT). In these latter cases, the transmitter and applicator pole were passed to the anglers' vessels during the fighting of the fish. Crew members then tagged the fish while the tracking vessel stood by ~100 m away. Once the fish had been released, tracking began.

To replicate tracks from one well-defined area, three tracks were initiated on the fishing grounds off Keahole Point, Hawaii. This is an area approximately 5 nautical miles (nmi) long and 2 nmi wide that is renowned for high catch rates of marlin during certain periods of the summer. For comparison, two other tracks were initiated from locations ~12 nmi south of the Keahole grounds, and one fish was tracked off Barbers Point, Oahu.

Results

Six Pacific blue marlin were tracked. The three Keahole fish were all caught within a 1-nmi radius over a span of 19 days in 1988; one track was 24 hours, and two were of 42 hours duration each (Fig. 2). In 1989,

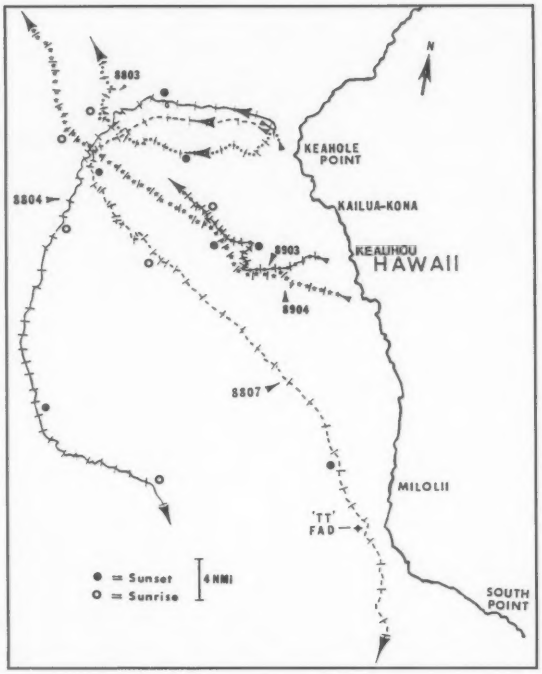

Figure 2
Horizontal movements of five Pacific blue marlin tagged off the Kona coast of Hawaii: three off Keahole Point and two off Keauhou. Lines perpendicular to the tracks represent hourly positions.

over a period of 4 days, two marlin were tracked from starting points ~4 nmi apart off Keauhou and were tracked for 26 and 29 hours (Fig. 2). The Barbers Point fish was tracked for 7 hours. Thus, all fish survived for at least 7 hours after release, and there is no reason to believe that any of the fish subsequently died as a result of the capture and tagging procedure.

Synopsis of tracks

Fish 8710 (weighing ~150 kg) was caught on a single-hooked artificial lure trolled behind the tracking vessel *Kaahele'ale* at a location 7 nmi west of Barbers Point, at 0904, 18 October 1987. After a fight time of 30 minutes, the fish was brought to the side of the boat. The fish was cleanly hooked through the bill and was immobile. The transmitter was embedded dorsolaterally, about a third of the way back along the dorsal fin. After release, the fish glided downwards and away from the boat and swam away on a southwesterly (offshore) course, which it maintained for the duration of the track. After 7 hours the fish was lost while at the surface. Data on the rate of horizontal movement for

Table 1
Rates of horizontal movement of captured and released Pacific blue marlin off Hawaii.

Track ID	Duration (hr)	Average speed (kn ± SD) Day	Night	Total	First hour
8710	7.0	1.21±0.27	NA	1.21±0.27	1.50
8803	24.0	1.48±0.31	1.37±0.32	1.43±0.30	1.20
8804	42.0	2.04±0.43	1.78±0.37	1.90±0.42	3.25
8807	42.0	2.25±0.67	2.09±0.67	2.18±0.65	3.25
8903	26.0	0.95±0.54	0.65±0.36	0.83±0.49	1.80
8904	29.0	1.62±0.37	1.68±0.39	1.65±0.37	3.00

this fish and the other five marlin are summarized in Table 1.

In terms of vertical behavior, this fish dove when released and spent the next 4 hours in the top 3 or 4 degrees of the thermocline at depths varying between 50 and 70 m. The fish then moved closer to the surface, spending 92% of the last 3 hours of the track within the surface mixed layer, moving between the surface and 35 m.

Fish 8803 (60 kg) was caught and tagged 2 nmi off Keahole Point at 1120, 8 August 1988, by a team participating in the HIBT. The fish was fought for ~20 minutes and described as tired but in good condition when released by the anglers. This marlin moved steadily west for ~12 hours before curving north during the night (Fig. 2). The fish was moving northwest when the track was terminated after 24 hours because of deteriorating sea conditions. The vertical movements of this fish (Fig. 3A) had a consistent "floor" where

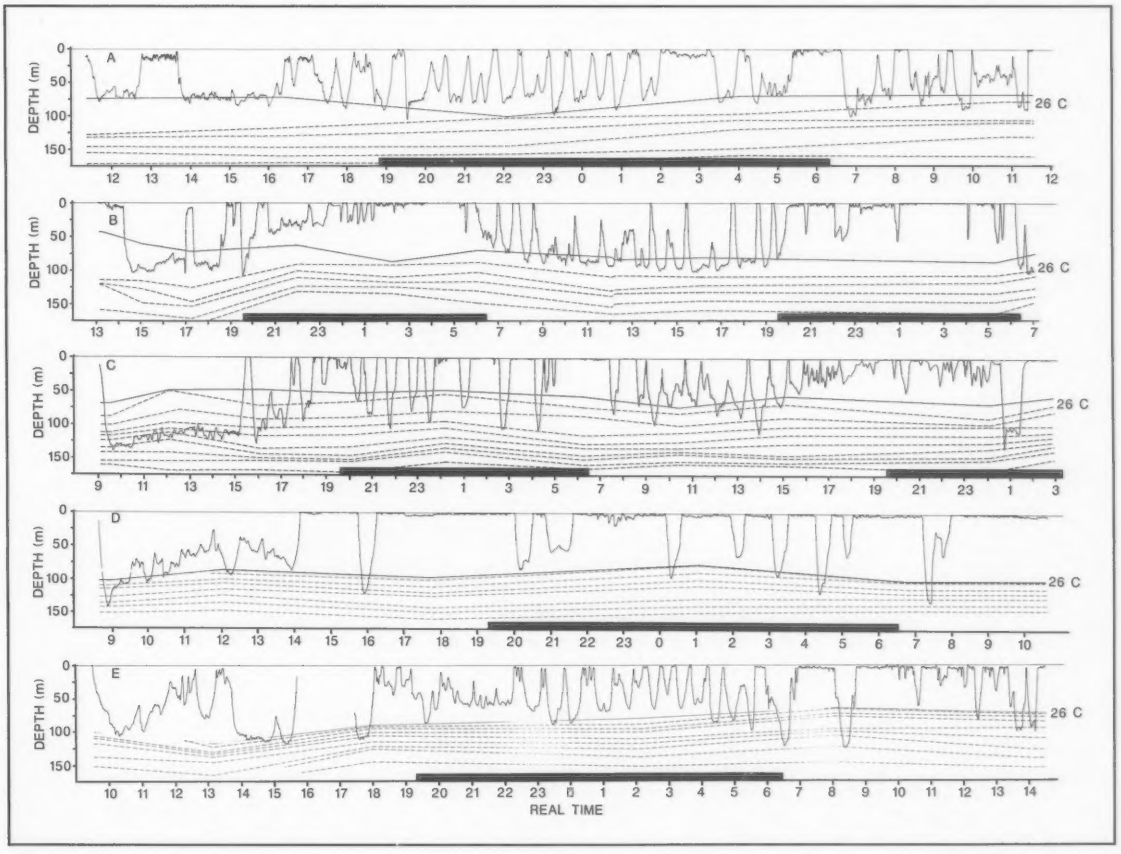

Figure 3
Vertical movements of marlin tracked off Keahole Point and Keauhou, Hawaii. A = fish 8803; B = 8804; C = 8807; D = 8903; E = 8904. Solid horizontal line represents the sharpest inflection in water temperature at the bottom of the mixed layer, whereas dashed horizontal lines represent 1°C isotherms, starting at 1°C below surface temperature. Horizontal bars represent nighttime.

the surface mixed layer met the top of the thermocline at depths varying between 75 and 100 m. During the daytime, the fish moved in and out of the top of the thermocline, with occasional excursions towards the surface; during the night, movements were more completely confined within the mixed layer with more time spent very close to the surface.

Fish 8804 (also estimated to weigh 60 kg) was caught and tagged by an HIBT team at 1310, 11 August 1988, 3 nmi off Keahole Point. Fight time and release condition were similar to fish 8803. After an initial, brief movement towards shore, this fish also proceeded directly west for about 8 hours before curving southward after sunset on the first night (Fig. 2). This direction was maintained all day during the second day until after sunset when it turned more shoreward. However, a southerly course was resumed after sunrise of the third day. The track was terminated after 42 hours.

The daytime vertical movements of this fish were focused around the interface between the mixed layer and the thermocline. From that depth (around 90 m) intermittent excursions were made to the surface. Nighttime distribution was shifted markedly towards the surface (Fig. 3B).

Fish 8807 was caught by the *Kaahele'ale* at 0900 on 27 August 1988, 3 nmi off Keahole Point. The fish, which was fought for 35 minutes, was caught using an artificial lure with a single hook that lodged in the base of the marlin's bill. The fish, weighing in excess of 160 kg, was completely immobile and floating belly-up at the side of the boat when the transmitter was attached near the midline in line with anterior insertion of the anal fin.

When the leader was cut, the fish sank slowly upside down under the boat but, after ~30 seconds, righted itself and began to swim slowly downwards. During the next hour, the fish traveled 3.25 nmi and, as with the previous two Keahole fish, headed steadily west, in this case for 7 hours. After sunset, the fish slowed and assumed a southeasterly course which it retained for the remainder of the track. After sunset on the second night, the fish returned close to the island and briefly visited fish aggregating device (FAD) TT off Milolii (Fig. 2). The fish was lost in rapidly deteriorating sea conditions off South Point, Hawaii, after 42 hours of tracking. At this time, the fish appeared to be continuing in a southerly direction.

Immediately upon release, this fish descended into the uppermost 2 or 3 degrees of the thermocline, where it remained for 6 hours as it swam steadily offshore. Upward excursions towards the surface started 3 hours before sunset, and movements on the second day were mostly in the thermocline-mixed layer interface with frequent upward movements, some of which reached the surface. As with the other Keahole marlin, nighttime distribution was shifted towards the surface, with considerable amounts of time spent at the surface (Fig. 3C).

Fish 8903, weighing ~75 kg, was caught and released 3 nmi off Keauhou Bay by a team in the 1989 HIBT. The fight time was ~20 minutes and the fish was lively when the transmitter was attached. Immediately upon release, the fish headed offshore for 5.5 hours before turning north (Fig. 2). This initial deviation in direction occurred ~11.5 nmi offshore and coincided with the marlin's first movement to the surface from the top of the thermocline, where it had been since the initial release (Fig. 3D).

Compared with other fish tracked in this study, this fish spent large amounts of time swimming slowly very close to the surface, often with the tips of its dorsal and caudal fins protruding above the surface. Although this "lazy" surface behavior is not uncommonly observed by fishermen, this was the only fish to demonstrate this behavior in the current study. The track was terminated after 24 hours, with the fish continuing to swim slowly at the surface in a northwesterly direction.

Fish 8904, also weighing ~75 kg, was caught and released by an HIBT team at a location ~2 nmi offshore of Kealakekua Bay, after a 36-minute fight. This fish also ran west (for ~6 hours) to a point 11.5 nmi offshore, at which time contact was lost for ~2 hours. When relocated, the fish had adopted a northwesterly course which it maintained for the remainder of the 29-hour track (Fig. 2). Vertical movements were similar to those of other fish, being largely constrained by the top of the thermocline and the surface, and averaging closer to the surface at night than during the day (Fig. 3E).

Temperature and depth distribution

Pooling the data from all six fish indicates that 82% of the daytime and 97% of nighttime distribution occurred in the mixed layer and top 2 degrees of the thermocline. In terms of depth, approximately 36% of the daytime and 60% of nighttime was spent between the surface and 30 m, the rest of the time being spent at greater depths (Fig. 4).

Discussion

Although the sample size reported here is quite small, these data represent a significant increase in the number of Pacific blue marlin tracked. Also, several aspects of the behavior of these marlin show remarkable consistency.

For instance, the behavior of all the fish tracked in this study was strongly influenced by the interface

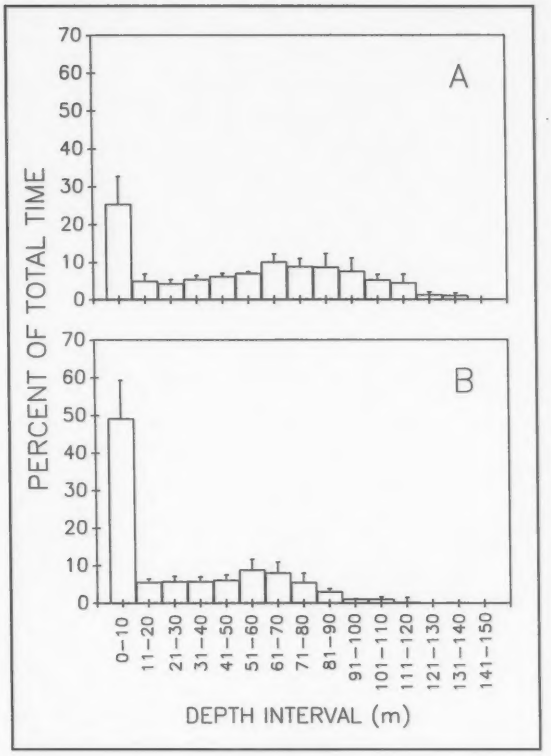

Figure 4

Aggregate depth distribution of six Pacific blue marlin off Hawaii during daytime (A) and nighttime (B).

between the surface mixed layer and the top few degrees of the thermocline, even though the depth of this interface varied between tracks. Unlike yellowfin tuna *Thunnus albacares*, which are also associated with this feature (Carey and Olson 1982, Yonemori 1982, Holland et al. In press), the marlin only rarely dove below the top of the thermocline. Thus, a major portion of the distribution of these marlin was bracketed by the surface and the bottom of the mixed layer. This behavior—not making deep dives, and spending most time in the mixed layer and upper thermocline—is similar to that of striped marlin tracked off California (Holts and Bedford In press), but differs greatly from that of swordfish which make frequent deep dives into cold water (Carey and Robison 1981). Compared with the striped marlin tracked off California, most of the blue marlin in Hawaii spent a relatively small amount of time very close to the surface. This may be due to the shallower depth of the thermocline off California (15–25 m) compared with Hawaii (35–90 m). With the exception of fish 8903, which spent an atypical amount of daytime very close to the surface, the marlin tracked in the present study moved closer to the surface at night. This differs from the striped marlin data, but is consistent with the behavior reported for skipjack tuna *Katsuwonus pelamis* (Yuen 1970), swordfish (Carey and Robison 1981), yellowfin tuna (Yonemori 1982, Holland et al. In press), and bigeye tuna *T. obesus* (Holland et al. In press).

Upon release, all six marlin dove into the upper layers of the thermocline and remained there for several hours. Onset of consistent upward excursions from the thermocline appeared to represent the end of the post-capture recovery period, usually between 4 to 6 hours. The recovery period was initiated by comparatively high-speed swimming, with four of the six fish travelling farther in the first hour following release than at any other time during the tracks. Because marlin are obligate ram-ventilators, these fish may be swimming fast enough to repay the anaerobic metabolic debt incurred during the fight, but not so fast as to acquire new debt. The fast speeds of the first hour are even more remarkable considering that at least two of the fish appeared to be completely exhausted when tagged and released. Holts and Bedford (In press) also report deeper than normal depths and heightened activity levels immediately upon the release of striped marlin.

With the exception of slow-moving fish 8903, the range of swimming speeds of individual fish in our study (1.2–2.18 kn) are similar to the blue marlin (1.2–1.9 kn) of Yuen et al. (1974). This is somewhat faster than the striped marlin speeds (0.75–1.45 kn) observed by Holts and Bedford (In press). In the present study, most of the fish swam slightly slower at night than during the day.

One of the most remarkable features of the current study is the consistent direction of movement displayed by the marlin in the first several hours of each track. Even though the three Keahole fish could have moved anywhere within a 240°-sector without running into land, all three swam along parallel westerly courses that took them directly offshore. Also, initial deviation from these parallel tracks occurred in the same general area ~12 nmi offshore. Similarly, both fish caught off Keauhou swam offshore for ~6 hours along almost identical paths, and both made their first major directional changes between 11 and 12 nmi offshore. This point in these two tracks was separated by only ~0.5 nmi, even though the release sites were over 4 nmi apart. The previously longest track of a Pacific blue marlin (22.5 hours; Yuen et al. 1974) was also initiated off Keauhou, and also commenced with a 7 nmi-movement offshore, as did the Barbers Point marlin tracked in the current study.

These results suggest that direct movement offshore may be a common response to the trauma associated

with capture and release. The first major horizontal direction changes often coincide with changes in vertical behavior and may represent the end of the recovery period.

Previous blue marlin tracks, and those acquired in the present study, share the characteristic of essentially straight or slowly curving azimuths. This contrasts with the movements of nearshore tuna (Yuen 1970, Holland et al. In press) and swordfish (Carey and Robison 1981) which frequently display cyclical diel movements that bring the fish back to their starting points. If Pacific blue marlin have such a pattern in Hawaiian waters, the cycle time for this behavior is longer than any of the tracks so far obtained. At present, the impression is that these animals swim along straight or slightly curving courses as they move through the area.

It is difficult to explain the difference in tagging mortality between this study in which no fish died and the previous one in which three of the five blue marlin died (Yuen et al. 1974). Holts and Bedford (In press) also report that none of their 11 striped marlin died as a result of tagging trauma. Their results, and the results reported here, support the practice of releasing marlin caught on artificial lures by sportfishing techniques, even if the fish are apparently exhausted.

Acknowledgments

This work was supported by the University of Hawaii Sea Grant Program (Ultrasonic telemetry of Horizontal and Vertical Movements of Pelagic Fish Associated with FADs, project MR/R-25) under Institutional Grant No. NA85AA-D-SG082 from the NOAA office of Sea Grant, Department of Commerce; the Honolulu Laboratory, National Marine Fisheries Service, NOAA; and the Hawaii Institute of Marine Biology, University of Hawaii. We also gratefully acknowledge the assistance of Lts.(jg.) Mark Ablondi and Scott Sullivan, NOAA; the Pacific Gamefish Research Foundation; the Hawaii International Billfish Foundation; and the anglers and captains of the 1988 and 1989 Hawaii International Billfish Tournaments.

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Diversity, Abundance, and Spatial Distribution of Fishes and Crustaceans in the Rocky Subtidal Zone of the Gulf of Maine*

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Shallow subtidal habitats of the Gulf of Maine harbor important populations of decapod crustaceans and a variety of fish species (Bigelow and Schroeder 1953, Cooper et al. 1975, Hacunda 1981). Because of the economic importance of lobsters, considerable work has been done on the biology and autecology of this species along the northwest Atlantic coast (see, for example, Campbell and Stasko 1986, and papers cited therein). Additional attention has been given to the study of lobster ecology since Mann and co-workers suggested in the 1970s that lobsters were "keystone predators" (sensu Paine 1969) in these systems (Mann and Breen 1972, Breen and Mann 1976, but see Miller 1985). There are relatively few published studies dealing with other common predators, such as fish and crabs, inhabiting shallow subtidal habitats of the coast of Maine. With few exceptions, most studies on fishes have dealt primarily with aspects of feeding and reproductive biology of single species (e.g., cunners: Chao 1973, Olla et al. 1975; sculpins: Moore and Moore 1974; wolffish and cod: Keats et al. 1986, 1987). Long-term temporal and spatial changes of demersal fish assemblages along this coast have been analyzed by Tyler (1971) and Hacunda (1981), and more recently, MacDonald et al. (1984) have studied temporal variation of inshore fish assemblages in Passamaquoddy Bay, Canada. To date, however, mobile predator assemblages (including fish and crustacean species) have not been comprehensively studied along the coast of the Gulf of Maine.

Our study first describes the composition of large mobile predators, particularly decapod crustaceans and fishes, occurring in rocky subtidal habitats at Pemaquid Point, Maine, and secondly examines their distribution, diversity, and abundance patterns on spatial (bathymetric) and temporal scales. The information gathered in this study is then analyzed in terms of seasonal impacts of those species in shallow rocky shores and the importance of these environments as nursery areas for these species.

Materials and methods

The study site was a rocky, shallow, sublittoral area off the southwest side of Pemaquid Point, Maine (43°50′N; 69°31′W). This is a wave-exposed area. The substrate down to ~10–12 m (below Mean Low Water Level, MLWL) consists of a sloping, relatively flat ledge. Large rocks and boulders characterize the bottom between ~12–20 m depth. At depths greater than 20 m the substrate is primarily sand with occasional boulders. A detailed description of this study area, including zonation patterns of benthic organisms, is given in Ojeda and Dearborn (1989).

Two methods were used to sample the mobile fauna of this region: gillnets and underwater observations. To determine diversity and abundance of fish species, two 3× 40 m experimental gillnets consisting of four panels (graded in mesh size from 10–20 mm to 60–70 mm) were randomly set in parallel on the bottom, perpendicular to the shore at depths between 5 and 23 m, and about 300 m apart.

Fish were sampled monthly for 2 to 3 days from June 1985 to October 1986, except in July, October, and December of 1985, and January 1986. Gillnets were usually set within the first hour after sunrise and retrived an hour before sunset. All captured fish were fixed in a 5–10% solution of buffered (borax) formalin-seawater mixture, placed in labeled plastic bags, and transported to the laboratory for further analysis. Preserved fish were identified, counted, measured (total length = TL) to the nearest 1.0 mm, and wet weighed to the nearest 1.0 g on a Mettler P1200 balance.

Temporal changes in fish abundance were determined by using a catch-per-unit-effort (CPUE) measurement. This index was calculated as the total number of fish captured

*Contribution of the Department of Zoology, Migratory Fish Research Institute, and Ira C. Darling Center of the University of Maine.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted 20 December 1989.
Fishery Bulletin, U.S. 88:403–410.

Table 1

List of fish species found in rocky subtidal habitats at Pemaquid Point, Maine. N = total number of individuals captured in gillnets; % = percent of captures.

	Common name	N	%	Size range (cm TL)
Class Chondrichthyes				
Squalus acanthias Linnaeus	spiny dogfish	42	6.7	87.0–118.0
Raja erinacea Mitchill	little skate	2	0.3	47.0–51.0
Class Osteichthyes				
Alosa sapidissima (Wilson)	American shad	11	1.8	27.5–38.5
Clupea harengus (Linnaeus)	Atlantic herring	2	0.3	6.2–6.4
Osmerus mordax (Mitchill)	smelt	2	0.3	21.7–22.7
Gadus morhua (Linnaeus)	cod	22	3.5	18.7–54.0
Microgadus tomcod (Walbaum)	tomcod	2	0.3	23.6–25.1
Pollachius virens (Linnaeus)	pollock	219	35.21	11.5–30.0
Merluccius bilinearis (Mitchill)	silver hake	4	0.6	15.2–18.2
Centropristis striata (Linnaeus)	black seabass	9	1.4	23.5–26.0
Pomatomus saltatrix (Linnaeus)	bluefish	6	1.0	60.0–86.0
Stenotomus chrysops (Linnaeus)	sculp	3	0.5	20.4–23.3
Tautogolabrus adspersus (Walbaum)	cunner	161	25.8	9.5–32.0
Scomber scombrus Linnaeus	mackerel	47	7.5	27.3–47.2
Pholis gunnelus (Linnaeus)	rock gunnel	*	—	—
Ulvaria subbifurcata (Storer)	radiated shanny	*	—	—
Hemitripterus americanus (Gmelin)	sea raven	22	3.5	23.2–46.0
Myoxocephalus aenaeus (Mitchill)	grubby	2	0.3	9.5–13.2
Myoxocephalus scorpius (Linnaeus)	shorthorn sculpin	26	4.2	20.3–33.0
Myoxocephalus octodecemspinosus (Mitchill)	longhorn sculpin	25	4.0	18.5–43.5
Cyclopterus lumpus Linnaeus	lumpfish	1	0.2	27.0
Limanda ferruginea (Storer)	yellowtail flounder	6	1.0	33.0–36.0
Pseudopleuronectes americanus (Walbaum)	winter flounder	10	1.6	18.5–20.0
Total		624		

* Not caught in nets.

in both nets divided by the total number of sampling hours in each month.

To determine the spatial distribution as well as temporal changes in abundance of fish, lobsters, and crabs, visual underwater censuses of these species were conducted during the day using SCUBA across bathymetric transects. A total of 34 transects were made during June, August, September, and November 1985, and February, April, June, July, September, and October 1986. Each transect extended from 0 to ~23 m below MLWL, 5 m wide and ~60–70 m long, covering an area of ~300–350 m^2. The transects were surveyed in segments covering each 3-m depth interval. Two divers independently searched each of these areas exhaustively (in ~20 minutes), recording the number of crabs, lobsters, and fish species (both mobile and benthic ones). Two night-dive transects were conducted during September 1985 to determine nocturnal activity patterns of mobile predators. Four additional transects were carried out in May 1985 to estimate substrate heterogeneity along the depth gradient. Each transect consisted of a polypropylene line extended over the rocky bottom from 0 to 23 m below MLWL. In each of these transects, at depth intervals of 3 m, we recorded the number of crevices, holes, and burrows (shelters) larger than 5 cm in aperture occurring to a distance of half a meter to the right and to the left of the line.

One-way ANOVA followed by a Student-Newman-Keuls (hereafter SNK) multiple comparison test (Sokal and Rohlf 1969) were employed for the detection of changes in abundance of predators and shelters (substrate heterogeneity) over the temporal and bathymetric gradients studied.

Results

Species composition

A total of 4 species of decapod crustaceans, including 1 lobster species (*Homarus americanus*) and three species of crabs (*Cancer irroratus*, *C. borealis*, and *Carcinus maenas*), and 23 species of fish (624 specimens) were captured or observed from June 1985 to October 1986 (Table 1).

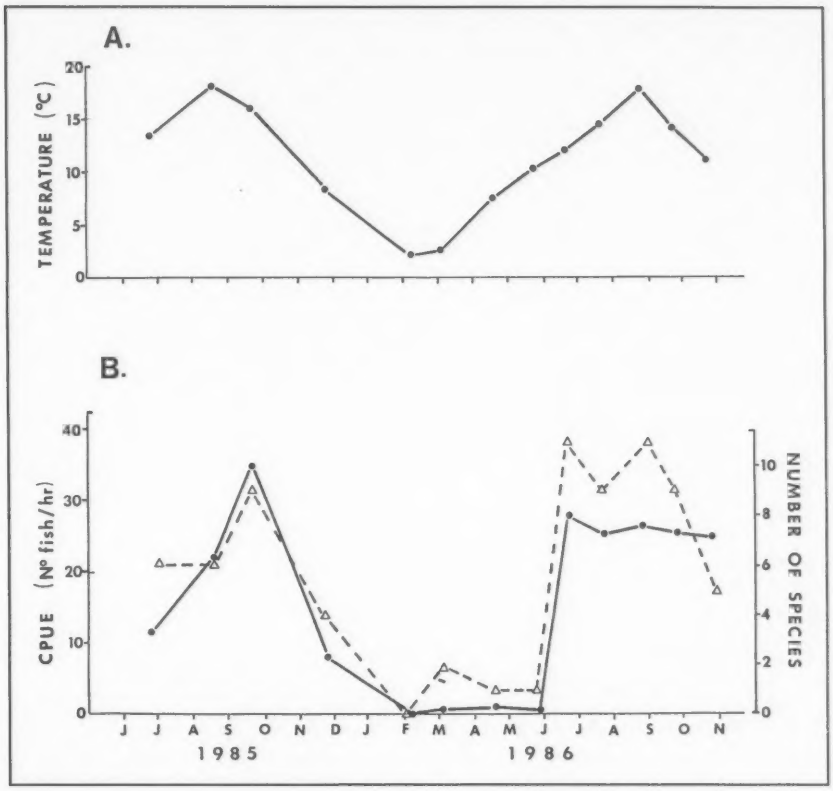

Figure 1
(A) Surface water temperature in Pemaquid Point, Maine, during 1985–86. (B) Temporal variation in the number of species (dashed line) and relative abundance (solid line) of fish captured with experimental gillnets at Pemaquid Point, Maine, during 1985–86. Abundances are expressed as captures per unit effort (CPUE).

The most abundant species were juvenile pollock and cunners (Table 1). Most of these pollock were immature individuals averaging 215 mm TL, which correspond to pollock of about 1 year-old (Bigelow and Schroeder 1953). Six other species were relatively common (represented by more than 2% and less than 10% of the total number of specimens collected: spiny dogfish, cod, mackerel, and sculpins). Most of the cod captured were juveniles averaging 300 mm TL, which correspond to an age of ~2 years (Bigelow and Schroeder 1953). Each of the remaining 13 species (61.9% of the total number of species) were represented by less than 2% of the total number of fish captured (Table 1).

Captures of all three sculpin species, pollock, and cod were significantly greater during the night than during the day (χ^2 test for goodness of fit, $P<0.05$) suggesting that these fish are primarily crepuscular and/or nocturnal predators.

On the other hand, cunners, mackerel, and spiny dogfish were captured almost equally during the day and at night ($P>0.05$). In contrast to mackerel and spiny dogfish, cunners were very rarely observed to be active at night, indicating they are primarily diurnal predators in these environments, as previously shown by Chao (1973), Olla et al. (1975), and Dew (1976).

Temporal patterns

Surface-water temperature of the littoral zone followed a seasonal cycle typical of cold waters of the Gulf of Maine (Fig. 1A), as shown by Tyler (1971) and MacDonald et al. (1984). Maximum values of about 18°C were observed during summer (July–September), and minima of about 1–2°C occurred during winter (February–March). Both the abundance and diversity of fish showed a clear seasonal pattern closely paralleling the seasonal variation of water temperature (Fig. 1B). Fish abundance peaked during summer, reaching values of 30–34 fish/hour, and was lowest (near zero) during winter. Species diversity followed a similar seasonal pattern (Fig. 1B). These results suggest a seasonal migration (inshore–offshore) of most components of this fish assemblage, which appears to be correlated with temperature changes.

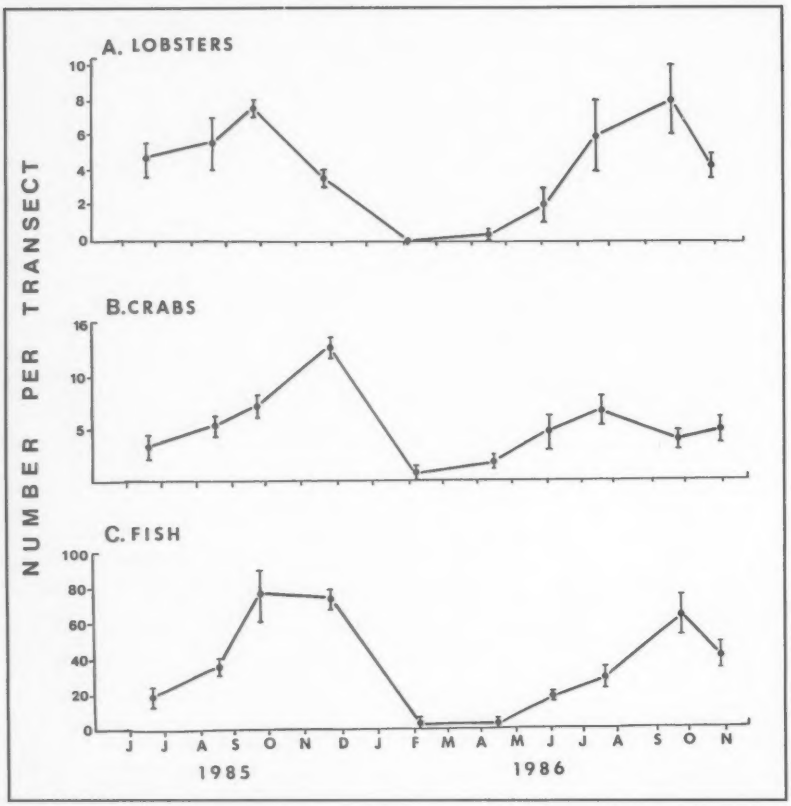

Figure 2
Seasonal variations in the abundance of lobsters (A), crabs (B), and benthic fish (C) along bathymetric underwater transects at Pemaquid Point, Maine. Each vertical bar indicates ±2 SE.

The abundance of major components of the catch—lobsters, crabs, and benthic fishes—also varied seasonally (one-way ANOVA, $P<0.01$ for all species; Fig. 2). Maximum abundances of lobsters occurred in summer (July–September) at densities of 5–8 individuals per transect (~1 adult lobster per 26 m^2) (Fig. 2A). No lobsters were observed in the winter transects (February 1986). The seasonal distribution of lobsters closely follows the seasonal variation in water temperature (compare Figures 1A and 2A). Highest densities of crabs, however, occurred in late fall (November) 1985, with ~14 individuals per transect (~1 adult crab per 12 m^2), and during the summer of 1986, though their densities were markedly lower than those observed in 1985 (~5 crabs per transect or ~1 crab per 33 m^2) (Fig. 2B). Few crabs were observed in winter; of those observed, most remained inactive and semiburied in the sand.

Benthic fish such as cunners, rock gunnels, sculpins, shannys, flounders, and rays were markedly most abundant during fall months, reaching densities of ~75 individuals per transect in 1985 and ~60 in 1986 (Fig. 2C). Their abundance decreased significantly in winter to 2–4 fish per transect, and progressively increased from mid-spring (May–June) until fall as temperature increased. Exhaustive underwater surveys for large predators were carried out in winter (February 1986) with the aid of underwater lights. No cunners or lobsters were observed along these transects despite the special care taken to examine crevices, caves, and spaces underneath boulders and rocks. In addition to a few crabs, three species of fish were commonly observed along these winter transects: rock gunnels, sea ravens, and winter flounders. Rock gunnels were the most abundant fish species, and they were usually observed up to 20 m depth, often associated with clumps of *Modiolus modiolus*. During the rest of the year, this fish species was rarely found at depths greater than 10 m.

This mobile predator assemblage can be divided into distinctive seasonal components. The first is comprised of "summer–fall residents," species consistently present from late spring until late fall, including pollock, cunners, longhorn and shorthorn sculpins, grubbys,

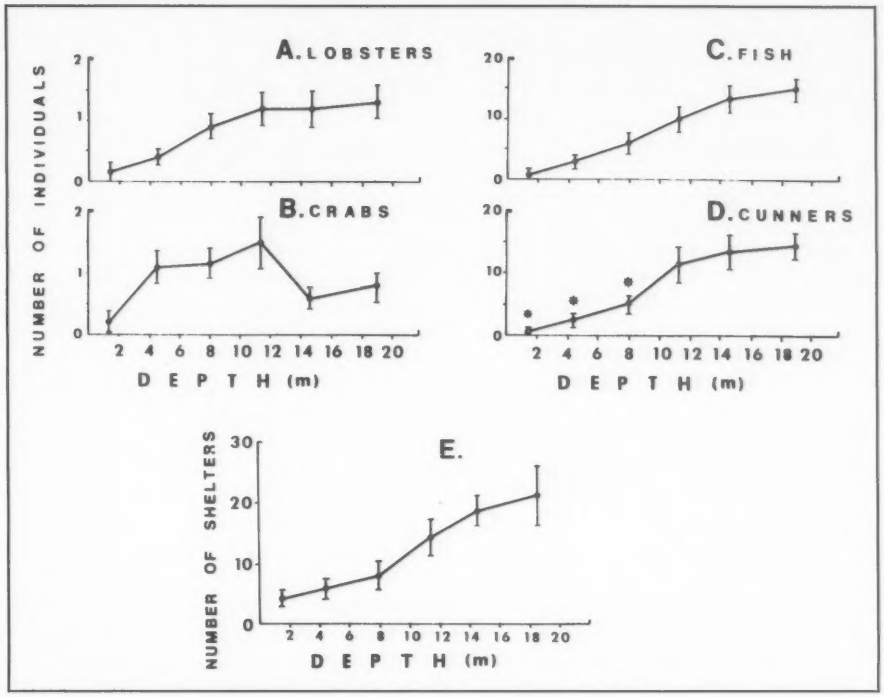

Figure 3
Bathymetric distribution in the abundances of lobsters (A), crabs (B), benthic fish (C), cunners (D), and number of shelters (E) in the underwater transects conducted at Pemaquid Point, Maine. Each vertical bar indicates ±2 SE. Asterisks in D indicate juvenile individuals.

cods, and lobsters and crabs. Lobsters and crabs, however, occurred earlier than these fishes. Crab species are included in this group because their abundance was extremely low during winter, and the few individuals that remained were not active. Summer–fall resident species moved into shallow water or became active (crabs) when the water temperature increased to 8–12°C, generally reaching maximum abundance in midsummer or early fall. The second component was the "regular residents," species captured or observed active at any season, such as sea ravens, rock gunnels, and winter flounders. These species, however, were generally much less abundant than the summer–fall residents (Table 1). The third temporal component of this fauna was the "summer periodicals" (sensu Tyler 1971), and refers to those species that occurred periodically in the samples during summer. The most abundant and conspicuous species in this group were mackerel, spiny dogfish, bluefish, and, less abundantly, black seabass and yellowtail flounder (Table 1). Finally, there was a group of species that occurred at infrequent intervals and in low numbers during this study. Fish species belonging to this group have been called "occasionals" (Tyler 1971) and include shad, little skate, lumpfish, scup, smelt, Atlantic herring, silver hake, and tomcod.

Spatial patterns

The abundances of most groups of mobile predators increased with depth, as did the number of shelters (Fig. 3). The number of adult lobsters significantly increased with depth in the first 8 m, then remained relatively constant thereafter to 19 m depth (one-way ANOVA, $P<0.01$; *a posteriori* SNK test; Fig. 3A). There was no relationship between depth and lobster size, since both large and small individuals were observed at all depths along the transects. Crab species (mostly *Cancer irroratus* and *C. borealis*) showed a somewhat different bathymetric pattern (Fig. 3B). Their abundance markedly increased between 2 and 5 m depth, remained relatively constant at 5–11 m, and decreased at depths greater than 14 m (one-way ANOVA, $P<0.01$, *a posteriori* SNK test). The collective abundance of benthic fishes (e.g., cunners, rock gunnels, radiated shannys, sculpins, and flounders) progressively increased along the bathymetric gradient, reaching highest density at the deeper zone (18–20 m depth; one-way ANOVA, $P<0.01$; *a posteriori* SNK test) (Fig. 3C). A large proportion of these fish, however, were cunners which comprised about 80% of the total number of individuals observed in the transects. Cunners exhibited a distribution pattern similar to the one described for total fish

(one-way ANOVA, $P<0.01$; *a posteriori* SNK test; Fig. 3D). In contrast to adult cunners, juvenile cunners (<5 cm) comprised more than 90% of the total cunners sighted in the first three depth stations (i.e., 2–8 m depth) along the transects.

The number of shelters (a measure of substrate heterogeneity) significantly increased with depth (one-way ANOVA, $P<0.01$; Fig. 3E). This increment is due to the increasing number of large rounded rocks observed at the deeper (10–20 m) transects which create large numbers of interstices (holes) suitable for predators' occurrence.

Discussion

A diverse assemblage of mobile predators inhabits the shallow rocky subtidal zone at Pemaquid Point, Maine. These subtidal habitats are utilized by these species for multiple purposes such as nursery grounds, feeding grounds, shelter, and reproductive activities (Olla et al. 1975, MacDonald et al. 1984, Keats et al. 1987, Ojeda 1987). The occurrence and abundance patterns of these species are, however, markedly seasonal and closely follow the temperature regime typical of northwest Atlantic waters. This suggests that temperature is one of the major abiotic factors affecting the distribution of these predator species on this coast, a finding in agreement with other studies (Tyler 1971; Hacunda 1981; Ennis 1984b; MacDonald et al. 1984; Keats et al. 1986, 1987).

Four temporally distinct components were recognized in this predator assemblage: summer–fall residents, regular residents, summer periodicals, and occasionals. Similarly, Tyler (1971) distinguished four temporal groups in the demersal fish assemblage occurring in Passamaquoddy Bay, New Brunswick, which have also been recognized in other demersal ichthyofaunas of the Gulf of Maine (Hacunda 1981, MacDonald et al. 1984). Three of the four categories of Tyler (1971) were recognized in this study: "regulars," "summer periodicals," and "occasionals." No representatives of Tyler's (1971) fourth category ("winter periodicals"; i.e., species occurring only during winter) were found in this study. This result, however, should be taken cautiously because no samples were taken in midwinter. The most conspicuous and abundant species of mobile predators in this study were summer–fall residents (e.g., cunners, pollock, lobsters, and sculpins), which occurred for most of the warm period in shallow rocky habitats. Summer–fall residents undergo small-scale migrations, moving into deeper, warmer water (>4°C) during winter and returning to shallow subtidal areas in spring. These seasonal movements occur in response to changes in water temperature and probably to physical disturbances such as strong water surges and storms along some exposed coasts. This seasonal migratory behavior represents a behavioral stratety to avoid freezing that involves no physiological adjustment. An alternative strategy involves the elaboration of macromolecules which possess unique antifreeze properties (e.g., glycopeptides in sea raven and winterflounder: Duman and De Vries 1974, Slaughter et al. 1981).

There are conflicting results in the literature concerning winter migration and activity of cunners and lobsters. Several authors have shown that cunners and lobsters do not migrate into deeper waters during winter (Green and Farwell 1971, Cooper et al. 1975, Olla et al. 1975, Dew 1976). However, investigations have shown that cunners (Chao 1973) and lobsters (Ennis 1984b) move to deeper waters in winter as suggested in this study. Recently, Ennis (1984b) showed that small-scale movements of lobsters in Newfoundland were related to increased turbulance due to storms. This is a likely explanation for the absence of lobsters and cunners during winter at Pemaquid Point in this study. As mentioned above, Pemaquid Point is an exposed site (Ojeda 1987). During winter, this area is severely affected by periodic storms and heavy water motion that usually generate strong turbulence over a wide depth range. For organisms that remain in dormant states in shallow waters during winter (such as cunners), water movements may severely restrict their distribution. Most studies documenting the presence of cunners in inshore habitats during winter have been conducted in bays or in other protected areas away from heavy water motion (e.g., Green and Farwell 1971, Olla et al. 1975, Dew 1976). In contrast, documentation of offshore movements of cunners during winter comes from studies conducted on exposed coasts, such as that of Chao (1973). A similar situation seems to occur in lobsters (Ennis 1984b) and probably with crab species which strongly suggests that water movement from turbulence and heavy surge is an important factor, in addition to water temperature, affecting the temporal and spatial distribution of large organisms in shallow subtidal environments of the Gulf of Maine.

Shallow rocky subtidal habitats along the northern New England coast harbor a diverse community of marine organisms providing abundant food resources to seasonal fish residents, occasional migratory fish species, and large crustacean predators (Ojeda 1987). This is so despite the general paucity of kelp beds in this coast, which are an important determinant of the abundance and diversity of nearshore fish and large decapod crustaceans on other temperate coasts (Quast 1968, Moreno and Jara 1984). In addition to acting as feeding grounds, shallow rocky environments also

provide large mobile predators with microhabitats for shelter against predation, and bases for reproductive activities and nursery grounds. Of particular relevance in these environments is the spatial heterogeneity of the bottom. Large rocks and boulders which typically occur at depths greater than 10 m at the study site are important microhabitats for territorial predatory species such as cunners and lobsters (Pottle and Green 1979, Ennis 1984a). The increased number of lobsters and fish (mostly cunners) observed along the bathymetric gradient is probably related to the availability of such microhabitats (see Figure 3). As shown elsewhere (Ojeda and Dearborn 1989), the substrate heterogeneity at Pemaquid Point progressively increases with depth as bottom irregularities such as cracks, crevices, holes, and rocks become more common. In addition to microhabitat availability, the observed bathymetric distribution of large predators may represent an avoidance response by these species to strong water turbulance and wave surge that commonly affect the shallower end of this subtidal zone (especially at low tides).

The occurrence in this study of numerous juvenile pollock and cod provides a good example of the importance of shallow, rocky, subtidal zones as nursery grounds as shown by MacDonald et al. (1984) and Keats et al. (1987). Juvenile pollock were the most abundant species of the nearshore fish assemblage (Table 1). These findings, in addition to feeding data presented elsewhere (Ojeda 1987), suggest that pelagic fish species may play important roles in rocky nearshore benthic communities by affecting the distribution and abundance of their benthic prey. Moreover, the one-way offshore migration exhibited by these species indicates that they may be important linkages in the transfer of energy from nearshore to offshore ecosystems.

Acknowledgments

This paper represents a portion of the Ph.D. dissertation submitted by F.P.O. to the Department of Zoology, University of Maine, Orono. We are grateful to Drs. Hugh DeWitt, Bob Elner, Bill Glanz, Fabian Jaksic, Irv Kornfield, and Les Watling, and to Dave Tapley for critically reading this paper. We appreciate the diving-assistance and logistic support given by I. Babb, M. Dunn, P. Garwood, C. Gregory, J. Guy, S. Hacker, D. Knowles, M. Lesser, C. Moody, G. Podniesisnski, B. Richardson, K. Scully, D. Tapley, R. Vadas, and R. Wahle. This research was funded by grants from the Migratory Fish Research Institute (MFRI), the Graduate Student Board (GSB), and the Department of Zoology (all of them to F.P.O.) of the University of Maine, Orono. The work of F.P.O. at the University of Maine was funded by an ODEPLAN Chilean Scholarship, by a University Graduate Research Fellowship, and by the Center for Marine Studies of the University of Maine.

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A Seasonal Autoregressive Model of the Anchovy *Engraulis encrasicolus* Fishery in the Eastern Mediterranean

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Accurate forecasting is a difficult issue mainly because forecasters are confronted by all sorts of uncertainty (in resource production, budgets, political decisions, etc.) (Hilborn 1987). Although not widely employed, Auto-Regressive Integrated Moving Average (ARIMA) stochastic models (Box and Jenkins 1976) have been successful in describing and forecasting the fishery dynamics of a wide variety of species (lobster: Boudreault et al. 1977, Saila et al. 1979; tuna: Mendelssohn 1981; pilchard: Stergiou 1989a). Although multivariate, deterministic models (e.g., regression models: Ryan 1986, Koslow et al. 1987) are more common in fishery forecasting, these deterministic models often suffer from (1) artificial correlations introduced to the data, (2) residual autocorrelation, (3) high residual variance, and (4) colinearity between the independent variables that may bias the fit (Stergiou 1989b, In press).

In this note, a seasonal autoregressive model is presented that produces forecasts of the monthly purse-seine catches of anchovy *Engraulis encrasicolus* in Greek waters. The anchovy is one of the most important pelagic fish, in terms of biomass, in the Mediteranean Sea. Mean annual anchovy catch in Greek waters during 1982–85 amounted to 12 820 t, representing 17% of the total marine catch (Stergiou 1989b). Of the anchovy catch in Greek waters, 96% is attributed to the purse-seine fishery, accounting for 26% of the total purse-seine catch (Stergiou 1986a, b). Monthly catches of anchovy for January 1964–December 1986 (Fig. 1) (National Statistical Service of Greece 1968–88) show a marked seasonal pattern (Figs. 1, 2) and an increasing trend in the variability of monthly catches for the years following 1980. The latter may indicate that anchovy has suffered recruitment overfishing in recent years (since the late 1970s, purse-seine fishing in Greek waters is anchovy-oriented rather than pilchard-oriented due to the higher price of anchovy [Stergiou 1986b, 1989a, 1990]).

The ARIMA processes (Box and Jenkins 1976, Makridakis et al. 1983) apply to stationary series (time series with no systematic change in mean and variance and free of periodic variations). First- or second-order differencing (nonseasonal and/or seasonal) handles problems of nonstationarity in the mean, and logarithmic (or power) transformation of the raw data handles nonstationary variance. The general form of the ARIMA models,

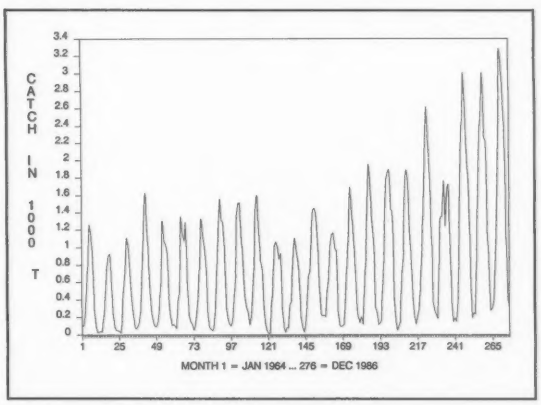

Figure 1
Monthly catches of anchovy in Greek waters, January 1964–December 1986.

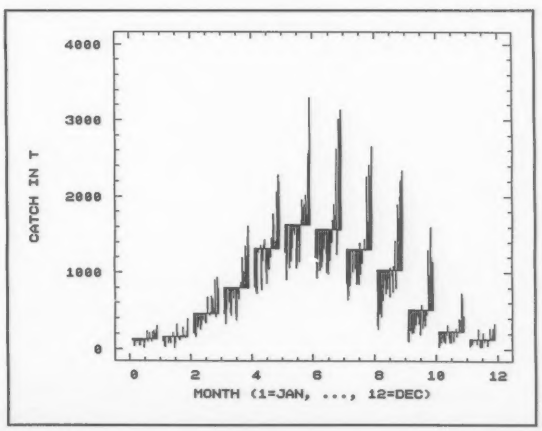

Figure 2
Seasonal subseries plot of monthly catches of anchovy in Greek waters, 1964–86. Horizontal lines represent the average catch of each month. Vertical lines are plotted from the average catch to the actual catch of each year of the 1964–86 period.

Manuscript accepted 28 December 1989.
Fishery Bulletin, U.S. 88:411–414.

$$\text{ARIMA } (p,d,q)(P,D,Q)^S,$$

can be described by the following equation:

$$(1-n_1B^p)(1-N_1B^P)$$

$$(1-B^d)(1-B^D)X_t = (1-u_1B^q)(1-U_1B^Q)e_t$$

where X_t = the value at time t, B^p is a backward shift operator that is used as $B^pX_t = X_{t-p}$, n_1, N_1, u_1, and U_1 = arithmetic coefficients, e_t = error term at time t, p = order of autoregressive term (AR term), d = degree of differencing involved to achieve stationarity (I term), q = order of moving average term (MA term), and S = seasonality (number of periods per season); P, D, Q = seasonal terms (corresponding to p,q,d respectively).

Based on the examination of autocorrelation and partial autocorrelation functions (not shown here) of the original logarithmically transformed series, the following model was fitted to the logarithms of the raw data,

$$\text{ARIMA } (1,1,0)(1,1,0)^{12} \text{ (Table 1)},$$

or, after substituting the autoregressive coefficients and expanding the backward shift operator (X_t = logarithm of raw data),

$$X_t = 0.792X_{t-1} - 0.208X_{t-2} + 0.684X_{t-12}$$

$$-0.862X_{t-13} + 0.138X_{t-14} + 0.336X_{t-24}$$

$$-0.266X_{t-25} - 0.07X_{t-26} + e_t.$$

The unit of time (t) is one month. The model was estimated using the approximate maximum-likelihood algorithm of McLeod and Sales (1983). Parameters were estimated using backcasting with length of 13.

The examination of the cumulative periodogram of the residuals (not shown here) (Box and Jenkins 1976) indicated that residuals approximated random noise. Actual catches for January 1985–December 1986, not used in the development of the model, and forecasts for those years are plotted in Figure 3. The coefficient of determination (Table 1) was found to be $r^2 = 0.94$ for January 1985–December 1986 (for the untransformed series).

Mean absolute percentage error (MAPE) (Table 1) for January 1985–December 1986 was 20.4%. Except for March and October 1985 and February, October and November 1986, when the absolute percentage error (APE) was higher than 26% (Table 1), monthly catches were predicted reasonably accurately within an APE range of 2–26% (MAPE of the remaining 19 forecasts was 11%) (Table 1).

Table 1

Parameter estimates of the anchovy fishery model. MAPE = mean absolute percentage error, APE = absolute percentage error, r^2 = coefficient of determination.

APE =

$$\frac{\text{Absolute (actual catch at time } t - \text{ forecast at time } t)\ 100}{\text{Actual catch at time } t}$$

MAPE = mean of APE, and

r^2 = 1 – (variance of residuals)/(variance of variable)

Parameter	Estimate	SE	Significance
n_1	−0.208	0.067	$p<0.01$
N_1	−0.336	0.059	$p<0.001$
r^2 for 1985–86		0.94	
Residual mean		0.007	
MAPE 1985		13.3	
MAPE 1986		27.4	
MAPE 1985–86		20.4	
APE>26%			
March 1985		31.5	
October 1985		33.5	
February 1986		47.7	
October 1986		65.9	
November 1986		95.6	
MAPE excluding APE>26		11	

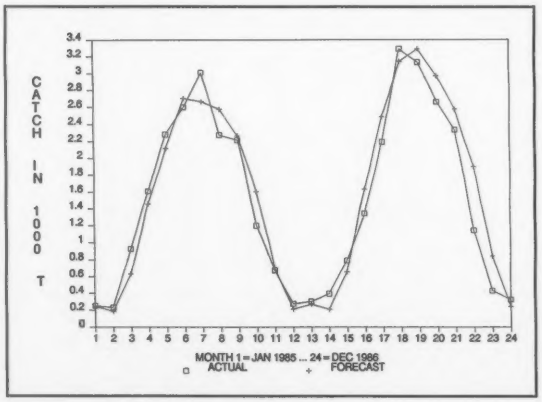

Figure 3

Comparison between actual monthly catches (□) of anchovy in Greek waters during January 1985–December 1986 and the forecasts (+) estimated from the model.

The error in predicting the February–March and October–November catches may be attributed to the highly variable timing of the initiation of the inshore (prespawning migration, which occurs sometime in March) and the offshore migrations (in fall) both of which are expected to be affected greatly by ocean-

ographic conditions. Catches exhibit a marked seasonal pattern (Figs. 1, 2) which is likely related to these seasonal offshore and inshore migrations. Purse-seine fishing activity in Greek waters does not operate in the open sea but is mainly restricted to coastal areas where schools of anchovy migrate on a seasonal basis. The anchovy starts its inshore migration in early spring, but the peak occurs in coastal waters in May–August and schools disperse again during late summer–fall (Fig. 2; Tsimenidis and Caragitsou 1984).

In Greek waters trawling and coastal seining are prohibited from the 1st of June to the 30th of September. As a result, the landings of demersal species (e.g., *Merluccius merluccius*, *Micromesistius poutassou*, *Lophius* sp., *Mullus* sp., *Pagellus* sp.) are low. This combined with the increased demand for fish in summer, drives up fish prices in Greece. In this context, accurate forecasts of the catches of anchovy (and of pelagic fish in general) during June–September are essential for market and industrial planning. APE in June–September was <11.2% in 1985 (mean 7.7%) and <10.6% in 1986 (mean 7.8%).

Strict monitoring and accurate forecasts are essential for pelagic fisheries that are heavily dependent on a single year-class, inasmuch as they are prone to collapse when conditions for recruitment in a particular year are not favorable and fishing is intense (as for anchovy in Greek waters). In this context, accurate forecasts of the annual anchovy catch together with information related to optimal management of anchovy estimated by deterministic fishery-management models, can be used by resource managers for the preseasonal adjustment of anchovy fishing mortality. The model produced reasonable forecasts of the annual 1985 and 1986 catches. Total observed annual catches in 1985 and 1986 were 17 544 t and 18 339 t, respectively, while the model predicted 17 369 t and 20 210 t (APE 1% and 10%, respectively). It must be pointed out, however, that although the model will most likely produce accurate forecasts if the anchovy stock is under equillibrium, it may fail to produce reliable forecasts for years characterized by weak year-classes of anchovy. (In fact there may be a lag of some months between the occurrence of a turning point and its recognition by the model; for a general discussion on turning points and out-of-sample forecasting, see Schlegel 1985.)

The model presented here has also an interesting biological interpretation. The seasonal-difference term of the model indicates the seasonal migratory nature of anchovy in Greek waters. Moreover, climate-plankton-anchovy interactions in the Eastern Mediterranean have been found to involve time lags of 2 to 3 years (Pucher-Petkovic et al. 1971). Yet, a 2–3 year cycle has been identified in the variability of different biotic (zooplankton, phytoplankton, fish) and abiotic (air and sea temperature, salinity and air pressure) components of the Eastern Mediterranean/Black Sea ecosystem (Polli 1955; Regner and Gacic 1974; S. Regner 1982, 1985; D. Regner 1985; Dement'Eva 1987; Petrova-Karadjova and Apostolov 1988). The autoregressive terms (X_{t-24}, X_{t-25}, X_{t-26}) of the model seem to be consistent with these biological/oceanographical observations.

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Tethering as a Technique for Assessing Predation Rates in Different Habitats: An Evaluation using Juvenile Lobsters *Homarus americanus*

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Tethering has been used successfully to assess predation rates of a variety of predator-prey systems in several different habitats. The majority of these experiments have used tethered crabs as prey (Heck and Thoman 1981, Wilson 1985, Wilson et al. 1987, Heck and Wilson 1988, Wilson et. al. 1990, Barshaw and Able In press). Fish have also been tethered in different habitats; however, in these experiments the tethered fish could not act naturally, and therefore the technique only showed the differences in predator encounter rate in different habitats (Shulman 1985, McIvor and Odum 1988). Other organisms are presently being used in tethering experiments including molluscs (R.N. Lipcius and L.S. Marshall, Jr., Coll. William and Mary, Va. Inst. Mar. Sci., Gloucester Pt., VA 23062, unpubl. data) and spiny lobsters (Herrnkind and Butler 1986).

We determined if tethering was an appropriate technique to assess predation on species that burrow (i.e., juvenile lobsters *Homarus americanus*). Lobsters were chosen for this study, in part, because their behavior has been well studied and, therefore, a baseline of "normal" behaviors is available (Botero and Atema 1982, Barshaw and Bryant-Rich 1988).

Lobsters use different methods of constructing burrows in different habitats; therefore we tested three habitats known to be important for early juvenile lobsters: mud, cobble, and *Spartina* peat (Able et al. 1988, Barshaw and Lavalli 1988).

Methods and materials

Six "ant farm" aquaria (10 cm wide, 30 cm long, 45 cm deep) were 2/3 filled with either cohesive mud, cobble of a natural size distribution, or *Spartina* peat substrates (two replicates per substrate type) and provided with running, unfiltered seawater. Early juvenile lobsters (8–14 mm carapace length) were individually tethered to monofilament line using "super glue" to attach it to their carapace. Individual tethered lobsters were placed into half the tanks while similar-sized untethered control lobsters were placed into the remaining tanks.

A discrete reading of each lobster's behavior was recorded every minute for the first 20 minutes, every 5 minutes for the next 35 minutes, and then every hour for 6 hours. A final assessment of each lobster's burrow was made after 24 hours. Therefore, each lobster was observed 33 times over 24 hours in each test. Seven tests were run using all the substrates, with two extra tests run only with mud; thus observations were made on a total of 14 lobsters in cobble, 14 in peat, and 26 in mud. The behaviors observed are described in Table 1.

The behaviors of the tethered and untethered lobsters were compared by calculating the percent of the 33 observations in which the lobsters were engaged in each of the behaviors for each test. Since this experiment was designed only to compare tethered and untethered lobsters, no comparisons were made between different behaviors or between different substrates (comparisons of that nature were studied in Barshaw and Bryant-Rich 1988). The percent of observations was transformed using the arc-sign transformation, and analyzed with a Student's t test. The numbers of the tethered and untethered lobsters that had burrows at the end of the experiment were analyzed for each substrate using 2×2 contingency tables and chi-square tests.

Results

The tethering of juvenile lobsters resulted in substrate-specific differences in behavior and the ability to construct burrows. There were no significant differences between the behavior of tethered and untethered lobsters in the peat or cobble substrates (Fig. 1); in both peat and cobble, all the tethered (7/7) and all the untethered (7/7) lobsters had burrows that they constructed and maintained throughout the experiment.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted 22 January 1990.
Fishery Bulletin, U.S. 88:415–417.

Table 1
Description of behaviors of tethered and untethered juvenile *Homarus americanus* observed in this experiment.

Behavior	Description
Rest (RST)	No movement for at least 30 seconds. Grooming was not considered movement and was not recorded separately from RST.
Pleopod fan (PPF)	Movement of the pleopods which caused sediment to be moved; i.e., was being used to build or repair the burrow. In this study PPF which only moved water was not recorded.
Bulldoze (BLD)	Pushing sediment forward with the claws and first walking legs spread apart.
Dig	Loosening sediment by pushing claws into it.
Walk (WLK)	Walking on the sediment; does not include "walking" in the burrow.
Swim	Swimming in the water column.

In the mud substrate, however, the tethered lobsters walked significantly more and bulldozed significantly less than the untethered lobsters (t test, $p<0.05$, Fig. 1). (There was a trend in the tethered lobsters to bulldoze less in all of the substrates). Also, in the mud substrate most tethered lobsters were unable to make or maintain a burrow. Only 7.7% (2/13) of the lobsters had constructed a complete burrow, deep enough to hide the lobster at the end of the 24-hour period. This result was significantly different from the untethered group in which 69.2% (9/13) had constructed burrows by the end of the experiment (chi-square test, $p<0.05$).

Discussion

These observations demonstrate a substrate-specific difference in the effect of tethering on the burrowing behavior of juvenile lobsters. While tethering did not substantially effect the behavior or burrow construction of lobsters in peat or cobble, lobsters tethered in mud spent more time walking, less time bulldozing, and were unable to build and maintain a burrow as well as the untethered lobsters. The tethered lobsters in mud would therefore be more vulnerable to predation than the untethered controls, since being without a burrow has been demonstrated to increase mortality due to predation (Barshaw and Lavalli 1988). Heck and Thoman (1981), Heck and Wilson (1988), and Barshaw and Able (In press) conducted predator-prey experiments using tethered crabs as the prey. *Neopanopi sayi*, *Panopeus herbsti*, *Libinia dubia*, *Ovalipes ocellatus*, and *Callinectes sapidus* were tethered using similar techniques as were used in our study. These investi-

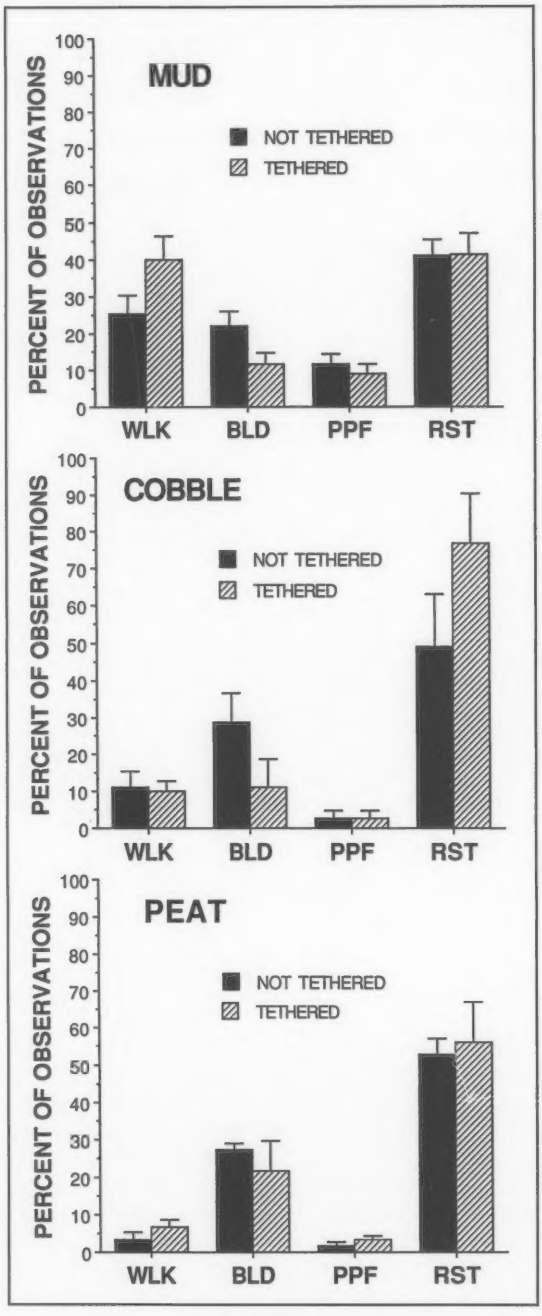

Figure 1
Average percent of the 33 observations in which lobsters were observed doing each behavior in each substrate. WLK = walk, BLD = bulldoze, PPF = pleopod fan, RST = rest.

gators did not observe any differences in the behavior of crabs tethered in different substrates. The differences in tethering effects between these investigations and ours are probably due to the fact that *Homarus americanus* construct burrows in the substrate while the crabs used in the above tethering experiments simply bury themselves directly into the substrate.

The results of this study suggest that tethering to assess predation in different habitats should be evaluated for each new species under consideration because species-specific behavior patterns could create habitat-specific tethering artifacts. In particular, caution should be used when interpreting survival rates of lobsters in mud relative to other substrates. Similar caution should be considered when tethering is used to assess predation in other burrowing forms.

Acknowledgments

We thank Donald Bryant-Rich, Dan Roelke, and Steve Weiss for help in collecting substrates and making observations. Mike Syslo and Kevin Johnson from the Martha's Vineyard State Lobster Hatchery and Kari Lavalli provided us with juvenile lobsters. Support for this study was provided by a minigrant from the New Jersey Marine Sciences Consortium.

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